



Advances in population ecology and species interactions in mammals

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The study of mammals has promoted the development and testing of many ideas in contemporary ecology. Here we address recent developments in foraging and habitat selection, source–sink dynamics, competition (both within and between species), population cycles, predation (including apparent competition), mutualism, and biological invasions. Because mammals are appealing to the public, ecological insight gleaned from the study of mammals has disproportionate potential in educating the public about ecological principles and their application to wise management. Mammals have been central to many computational and statistical developments in recent years, including refinements to traditional approaches and metrics (e.g., capture-recapture) as well as advancements of novel and developing fields (e.g., spatial capture-recapture, occupancy modeling, integrated population models). The study of mammals also poses challenges in terms of fully characterizing dynamics in natural conditions. Ongoing climate change threatens to affect global ecosystems, and mammals provide visible and charismatic subjects for research on local and regional effects of such change as well as predictive modeling of the long-term effects on ecosystem function and stability. Although much remains to be done, the population ecology of mammals continues to be a vibrant and rapidly developing field. We anticipate that the next quarter century will prove as exciting and productive for the study of mammals as has the recent one.

El estudio de los mamíferos ha promovido el desarrollo y puesta a prueba de muchas ideas en ecología contemporánea. En este trabajo, abordamos los nuevos avances sobre la selección de alimentación y de hábitat, dinámica fuente-sumidero, competencia (tanto dentro como entre especies), ciclos poblacionales, depredación (incluyendo competencia aparente), mutualismo e invasiones biológicas. Dado que los mamíferos son particularmente atractivos e interesantes para el público, el conocimiento ecológico resultante del estudio de los mamíferos tiene un alto potencial en educar al público sobre los principios ecológicos y su aplicación al manejo racional. Los mamíferos han sido claves para desarrollar muchos modelos computacionales y estadísticos en los últimos años, incluyendo mejoras a los enfoques y métricas tradicionales (por ejemplo, captura y recaptura) y avances en campos nuevos y en desarrollo (por ejemplo, captura y recaptura espacial, modelos de ocupación, modelos integrados de poblaciones). El estudio de los mamíferos también plantea retos en cuanto a la caracterización exhaustiva de dinámicas en condiciones naturales. El cambio climático amenaza con impactar ecosistemas a nivel mundial, y los mamíferos son sujetos visibles y carismáticos para la investigación de estos impactos, tanto a nivel local como regional y para el modelado predictivo de los efectos a largo plazo sobre la función y estabilidad del ecosistema. Aunque queda mucho por hacer, la ecología poblacional de mamíferos sigue siendo un campo vibrante y de rápido crecimiento. Anticipamos que el próximo cuarto de siglo será tan emocionante y productivo para el estudio de los mamíferos como lo ha sido recientemente.

Key words: competition, foraging, habitat selection, metapopulations, mutualism, population cycles, predation, quantitative ecology, source–sink dynamics

Mammals have been central subjects throughout the development of vertebrate ecology. Their interactions within and among species have provided extensive material for both theoretical and empirical ecologists. In the American Society of Mammalogists (ASM) 75th anniversary volume, [Lidicker \(1994:324\)](#) reviewed “how research on mammals over the last 75 years has influenced population ecology and . . . how developments in ecology generally have impacted mammalogy.” He argued that mammals and mammalogists are at the “front lines” of the most interesting and important themes in contemporary ecology. Noting that (p. 340) “mammals are among the more complex inhabitants of the planet,” they tend to be “larger and cleverer than most creatures . . . often represent[ing] keystone species,” and that they “often can serve as indicator species for the status and stability of intractably complex chunks of the biosphere,” [Lidicker \(1994\)](#) made a cogent case that understanding the ecology of mammals has greater implications than merely an improved understanding of science. We will largely build from the foundation established by [Lidicker \(1994\)](#) to summarize the key conceptual and practical results of research on mammals over the past 2 to 3 decades. We address three general themes. Following discussion of ecological fields rooted in behavioral ecology (foraging ecology, habitat selection), we move to themes operating primarily at the population level (including recent advances in population estimation, intraspecific competition, source–sink dynamics, and population cycles). We then present four contributions that emphasize interactions within or among species (interspecific competition, predation, mutualisms, and invasive species).

Humans rely on many mammals for food, clothing, and other resources, and mammals remain among the most popular attractions at zoological gardens and national parks. Moreover, wild mammals comprise a large proportion of “flagship” or “umbrella” species, reflecting their importance in conservation science (e.g., [Caro 2010](#)). Continued maturation of mammalian ecology is essential to enlightened management of wild populations in the face of climate change and other anthropogenic influences.

BEHAVIORAL MECHANISMS UNDERLYING POPULATIONS

Foraging Ecology

Foraging describes how an organism chooses to sample and capture resources. Because foraging focuses on choice, it is an inherently behavioral dynamic, often dealing with relatively short time scales (e.g., which foods will an animal eat today) and relatively small spatial scales (e.g., which portion of the home range will be searched for food). Unsuccessful foraging leads to death via starvation, predation, or disease, all of which curtail reproductive success. Because foraging describes daily choices that determine individual fitness, foraging ecology effectively links individual behavior to ecological and evolutionary processes, such as competitive interactions, predator–prey interactions, and rates of adaptation.

An individual-based perspective on foraging and the value of information.—Individuals should forage in a way that

maximizes their fitness ([Stephens and Krebs 1986](#); [Stephens et al. 2007](#)). Often, this requires balancing several objectives, such as increasing resource acquisition, reducing energy and time expenditure, and reducing the risk of injury or death. Achieving these goals requires that individuals be capable of detecting variation in resource quality ([Newman 2007](#)) and the likelihood of predation, parasitism, or disease ([Brown and Kotler 2007](#)). They should be sensitive to the metabolic costs of foraging, and be responsive to opportunities that they are missing while allocating foraging effort to a particular activity ([Brown and Kotler 2007](#)).

General principles.—Foraging ecology has an extensive literature and continues to attract much attention, both theoretical and empirical. This literature can be structured according to several related topical areas.

1) Information is critical to successful foraging.—Information reduces ambiguity regarding the true present or future state of the world ([Dall et al. 2005](#)), and thus of the costs and benefits of a particular action (see [Stephens et al. 2007](#) for an overview of signal detection). Mammals use diverse informative cues to modify their foraging activities ([Apfelbach et al. 2005](#); [Caro 2005](#)), drawing from many sensory modalities ([Weissburg et al. 2014](#)). For example, low environmental temperature may increase metabolic costs of foraging, and may alter forager activity ([Orrock and Danielson 2009](#)). Nights with precipitation, cloud cover, or low illumination (e.g., dark lunar phases) may signal reduced predation risk, leading to changes in foraging (e.g., [Prugh and Golden 2014](#)). Complex habitat features (e.g., downed woody debris, areas of thick vegetative cover) may signal areas where predation risk is reduced, leading to spatial ([Brown and Kotler 2004](#); [Mattos and Orrock 2010](#)) or temporal ([Connolly and Orrock 2018](#)) adjustments to foraging activity. Conditions that promote high relative humidity (e.g., recent rainfall) may signal more efficient foraging opportunities because moist soil conditions lead to increased production and transmission of olfactory cues that may facilitate detection of food ([Vander Wall 1998](#)). Animals also integrate information about themselves into their foraging activities; e.g., mammalian foraging often depends on individual state, such as hunger, reproductive condition, and mating status ([Stankowich and Blumstein 2005](#); [Newman 2007](#); [Kotler et al. 2010](#); [Prugh and Golden 2014](#)).

2) Predation risk is a fundamental component of the choices that foragers make.—Predation risk plays a critical role in how, when, and where animals forage. A large body of literature attests to an “ecology of fear” ([Brown et al. 1999](#); [Preisser et al. 2005](#); [Brown and Kotler 2007](#)). A seminal contribution to this discipline was the development of theory that linked risk with energy capture and fitness ([Brown 1988](#)), demonstrating how experiments could be used to understand how animals alter foraging to balance resource capture, predation risk, and missed-opportunity costs. Predation risk shapes the foraging of many mammals (e.g., [Brown and Kotler 2004](#); [Caro 2005](#); [Verdolin 2006](#); [Steele et al. 2014](#)). Foraging mammals also are cognizant of the risk of parasitism; white-tailed deer (*Odocoileus virginianus*) and domestic sheep (*Ovis aries*) alter foraging to reduce

the likelihood of encountering parasites (Hutchings et al. 2001; Allan et al. 2010b).

3) Resource quality is important, and often depends on constraints.—A classic model of optimal foraging (Charnov 1976) demonstrated that animals should consume prey items that yield the greatest energy per unit time, subject to handling and encounter rates. This model is instructive for highlighting key components of resources that may be important for foraging mammals, and receives some support from studies with mammals (Sih and Christensen 2001). Other factors that affect whether foraging mammals select a particular resource have been studied in grazing mammals, demonstrating that foraging mammals can differentiate between potential food items based on energetic value, spatial distribution, and toxin content (Bryant et al. 1991; Newman 2007; McArthur et al. 2014). In some cases, the value of food items may depend on environmental conditions, such as temperature or proximity to water (Newman 2007). Temporal considerations are also important. Hungry animals should become increasingly less selective in foraging, as well as increasingly willing to sample patches with high-variance outcomes. The effect of resource quality on foraging may also depend on predation risk (McArthur et al. 2014), with animals willing to forgo high-quality resources during periods of high risk (Lima and Bednekoff 1999). For predatory mammals, the quality of a particular prey item may not be accurately reflected in its caloric or nutritional value, but may hinge on the likelihood of successfully encountering, capturing, or subduing a particular prey item (Sih and Christensen 2001; Caro 2005; Brown and Kotler 2007; Stephens et al. 2007).

4) Individual-level variation matters.—Empirical evidence demonstrates considerable variation in foraging behavior (Sih et al. 2004; Stephens et al. 2007), and some of this variation may be predictable. Foragers may exhibit consistent phenotypes (i.e., behavioral syndromes, akin to an animal personality) that provide insight into within-species variation (Sih et al. 2004). For example, “fearful” prey may consistently exhibit a strong reduction in foraging in response to predation risk, and may be less likely to explore novel habitats, while “bold” phenotypes of the same species exhibit the opposite foraging pattern. Similarly, models (Stephens et al. 2007) and empirical studies (Galef and Giraldeau 2001; Caro 2005; Stankowich and Blumstein 2005; Preisser and Orrock 2012) that examine the role of individual state may explain variation in foraging among individuals as well as changes in foraging within an individual’s lifetime. For instance, hungry animals may tolerate greater predation risk when foraging (Caro 2005; Stankowich and Blumstein 2005), and young animals often exhibit different dietary preferences than older animals as a result of different nutritional needs, differences in experience, and other factors (Galef and Giraldeau 2001; Newman 2007). Maternal effects (i.e., maternally generated transgenerational phenotypic plasticity) may influence offspring foraging behavior (Maestripietri and Mateo 2009; Sheriff et al. 2018). For example, offspring born to mothers that experienced reduced food availability exhibit more fearful and less exploratory behavior than do

offspring of mothers who experienced higher food availability; maternal diet typically has a positive effect on food selection by offspring, with a variety of species tending to consume foods consumed by their mothers (Maestripietri and Mateo 2009; Sheriff et al. 2018). Cultural transmission of information and social processes may also modify foraging in many mammalian groups (Galef and Giraldeau 2001; Caro 2005). For example, several small mammal species make food choices based on assessment of the physical condition of conspecifics and the foods that they have eaten (Galef and Giraldeau 2001). Similarly, lambs (*O. aries*) select foods based on observing what their mothers eat (Newman 2007). Moreover, grazing mammals exhibit different food preferences when they are foraging in a large versus a small group (Newman 2007). Variation in foraging by primates may be a function of individual status, experience, social interactions, group size, cultural transmission (Galef and Giraldeau 2001; Trapanese et al., *In press*), and interactions with other vertebrates (Heymann and Hsia 2015).

Population- and community-level consequences of individual foraging.—Foraging choices made by individuals can alter ecological dynamics at multiple scales (Brown and Kotler 2007; Holt and Kimbrell 2007). When individuals alter their foraging in response to predation risk, reduced resource capture and increased physiological stress can reduce reproduction and survival, such that changes in individual foraging lead to changes in population size and persistence (Holt and Kimbrell 2007). For example, predator-mediated shifts in foraging may be important drivers of elk (*Cervus canadensis*) population dynamics, as they move to wooded cover where they are constrained to browsing (rather than preferred grazing) in the presence of gray wolves (*Canis lupus*—Creel et al. 2009). Populations may also decline when organisms make suboptimal foraging decisions because previously reliable clues are no longer reliable due to rapid environmental change. Animals are then caught in an “evolutionary trap” whereby use of previously informative cues leads to suboptimal decisions in the contemporary environment (Schlaepfer et al. 2005). Decisions made by animals exposed to novel species may also be viewed from the perspective of an evolutionary trap (Schlaepfer et al. 2005) because animals may fail to recognize introduced predators as dangerous (Blumstein and Daniel 2005), resulting in poor foraging choices that potentially lead to rapid population declines (Sih et al. 2010).

Foraging patterns may influence community-level phenomena, including direct effects such as competition and predation, as well as indirect effects such as trophic cascades (Brown and Kotler 2007; Estes et al. 2011) and apparent competition (Holt 1977; Holt and Bonsall 2017). Competition may be shaped by predation risk (Brown and Kotler 2007), with shifts in foraging due to the presence of one predator affecting susceptibility to other predators, thereby changing the outcome of predator–prey interactions (Sih et al. 1998). Examples of community-level effects of apparent competition include situations where invasive plants provide food and safety for white-tailed deer and several rodent species, leading to shifts in foraging activity (e.g., Dutra et al. 2011; Guiden and Orrock

2017), changes in native plant community composition (Orrock et al. 2015), and potential alteration of transmission of tick-borne disease (Allan et al. 2010a). Because predation risk can be such a strong, general driver of mammalian foraging, interactions driven by predation risk may be common in a variety of systems. For example, changes in common impala (*Aepyceros melampus*) foraging behavior in response to risk of predation by common leopards (*Panthera pardus*) and wild dogs (*Lycaon pictus*) can change plant communities, depending on the distribution of refuge-providing plants (Ford et al. 2014). Shifts in the foraging behavior of sea otters (*Enhydra lutris*—Estes et al. 1998), dugongs (*Dugong dugon*—Wirsing et al. 2007), and dolphins (*Tursiops aduncus*—Heithaus and Dill 2006) in response to predation risk can drive trophic cascades in aquatic systems (for a review in marine systems, see Kiszka et al. 2015).

Conceptual advances and technological innovations.—Over the past 25 years, several key theoretical, statistical, and methodological advances have helped advance knowledge of mammalian foraging. Although much early optimal foraging theory focused on selecting optimal diet components (Stephens and Krebs 1986), recent advances (Stephens et al. 2007) have broadened the focus to incorporate variation in information transfer (Bednekoff 2007), temporal variation in predation risk and prey state (Lima and Bednekoff 1999; Bednekoff 2007), the role of anthropogenic factors in affecting mammalian foraging (Gaynor et al. 2018), and the interplay of the metabolic costs of foraging, predation risk, and missed-opportunity costs (Brown 1988). Indeed, the giving-up density (GUD) framework (Brown 1988) has proven incredibly useful for evaluating foraging because it can be expanded to include additional factors (reviewed in Brown and Kotler 2004; Bedoya-Perez et al. 2013), such as variation in food quality under risk of predation (Schmidt 2000) or parasitism (Allan et al. 2010b). This framework is amenable to experimental approaches, making it possible to evaluate different costs of foraging in an integrated manner. For example, experiments can simultaneously quantify the energetic costs of competition and predation, making it possible to determine which is more important in a particular situation (Brown and Kotler 2007). Dynamic individual-based models have facilitated the evaluation of foraging decisions over the entire life of an organism, making it possible to understand the utility of foraging strategies that change with individual state and in response to temporal variation in resources (Grimm and Railsback 2005). Conceptual perspectives based on how risk- and energy-mediated changes in foraging can lead to larger-scale patterns of animal movement (Gallagher et al. 2017) further illustrate ways that factors affecting foraging may be productively integrated to make field-based predictions.

Statistical advances have helped elucidate broad-scale patterns in mammalian foraging and test predictions from theoretical models. Specifically, the development and widespread use of meta-analyses has made it possible to examine data from many studies to test hypotheses with broad taxonomic relevance. For example, meta-analyses have shaped our understanding of the effect of predation risk on foraging (Stankowich and Blumstein

2005; Verdolin 2006; Preisser and Orrock 2012), the utility of the optimal diet model (Sih and Christensen 2001), the effect of temporal variation in predation risk on foraging (Ferrari et al. 2009), and the influence of lunar illumination on mammalian responses to predation risk (Prugh and Golden 2014).

Understanding of mammalian foraging ecology has benefited from recent technological advances. Patterns of diet choice can be evaluated using markers such as fluorescent dyes (Fisher 1999), stable isotopes (Ben-David and Flaherty 2012), and DNA barcoding (Schneider et al. 2017). The ability to collect automated individual-level movement data (Cagnacci et al. 2010) can provide an in-depth perspective on spatial and temporal variation in foraging activity, even for organisms that move over large spatial extents. Remote cameras can be used to examine space use and activity timing (Burton et al. 2015). For small mammals, a new logger-based approach can allow researchers to easily match activity timing to particular individuals using standard livetrapping (Orrock and Connolly 2016). Automated PIT-tag readers now allow the collection of fine-scale spatial and temporal data (Kotler et al. 2010), and unmanned aerial vehicles (i.e., drones) also show considerable promise (Anderson and Gaston 2013).

Habitat Selection

Where an individual chooses to live is one of the most important decisions it can make, affecting survival, reproduction, foraging success, physical condition, and virtually all components of fitness. Numerous environmental factors can influence that decision. Thus, habitat selection is linked to almost every area of ecology, is fundamental to conservation and management, and may provide a unifying, general principle in ecology (Morris 2003b). Given that habitat selection is an adaptive strategy with fitness consequences, Morris (2003b) provides models of habitat selection as evolutionary strategies, mechanisms of population regulation, consequences of (and measures of) intra- and interspecific competition, factors affecting the distributions of predators and prey, and sources of biodiversity. A Google Scholar search using the terms “habitat selection” and “mammal” uncovered 39,600 references (accessed 25 January 2018) and limiting the search to the years 1994–2017 reduced that to a “mere” 21,100. Because of the volume of literature potentially bearing on this subject, we focus on studies that were intended to inform conservation and management. In recognition of the 100th anniversary of the ASM, we highlight articles from the *Journal of Mammalogy* (*JM*) over the past 30 years (1988–2017) as much as possible. About 12% of the papers published in *JM* during the past decade have involved analyses of habitat selection (Table 1).

Habitat is an area that includes the resources and physical conditions that permit the existence of a species (Morrison et al. 2006; Guthery and Strickland 2015). It may be subdivided into categories such as habitat for denning, breeding, foraging, or seasonal needs. However, the term “habitat” has been used in so many contexts and with so many modifiers that a rigorous definition is elusive (e.g., Guthery and Strickland 2015; Mathewson and Morrison 2015).

Habitat selection is a behavioral process that results in non-random use of available features of the environment. It differs from habitat use, which is a description of the types of environmental features used, and may include the proportions of time or locations associated with various environmental features, but does not relate these to availability. It also differs from habitat preference, which describes what an individual would choose in the absence of constraints such as predation risk or competition, and if all options were similarly available. For example, an individual might prefer to use certain features of an area, but is behaviorally inhibited from doing so. Inferring preference can only be done experimentally or by comparison of selection in areas with and without certain constraining factors (e.g., predators, competitors, ease of access). These definitions conform to a stepwise behavioral process wherein preference (unconstrained choice under ideal conditions) is a factor influencing selection (observed choice under existing conditions).

Only a few decades ago (1988–1997), most studies concerning habitat selection in *JM* focused on small mammals, used livetrapping as a field method, analyzed habitat data (usually vegetation, soil, and other characteristics in the vicinity of trap sites), and employed proportional statistics to compare use to availability or applied multivariate ordination methods (Table 1). Advances in methods for determining animal location include refinements to radiotelemetry technology, such as miniaturization of transmitters, allowing for their use on bats and small terrestrial mammals, and satellite-based global positioning system (GPS) transmitters that can record continual movements of multiple individuals; automatically triggered cameras that can noninvasively record the presence of a variety of species without relying on physical capture; microphones and software to record and analyze acoustic signals; and noninvasive genetic techniques for determining species presence based on scats, hair samples, or environmental DNA. As technology

Table 1.—Publications including habitat selection as feature articles in the *Journal of Mammalogy* (1988–2017). General groups of mammals, methods of obtaining data on locations of mammals (primarily field methods, but including a small number of studies that extracted data from published studies), and general categories of statistical analysis are presented. Numbers of taxa, field methods, and statistical methods do not sum to the number of studies because some studies included more than one taxon or method. “Other” under Statistical methods are primarily descriptive studies that do not include analyses based on availability, and therefore are studies of habitat use rather than selection, but were included in the table for their contributions to categories of taxa and field methods.

	1988–1992	1993–1997	1998–2002	2003–2007	2008–2012	2013–2017
Total articles	369	550	531	683	649	647
Habitat selection (%)	22 (6)	16 (2.9)	31 (5.8)	54 (7.9)	75 (11.6)	83 (12.8)
Taxa						
Small mammals ^a	15	8	13	19	31	28
Bats	2	3	6	10	9	12
Carnivorans	1	3	5	15	22	22
Ungulates	2	2	7	10	8	15
Other ^b	2	0	1	4	6	9
Field methods						
Livetrapping	14	5	9	13	18	13
Sign, direct observation ^c	5	4	10	14	20	20
Telemetry	4	6	9	25	31	32
Cameras	0	0	0	1	4	14
Museum or other literature	1	0	0	1	1	1
Other ^d	2	1	4	4	3	7
Statistical methods						
Proportional ^e	10	8	16	34	37	28
Ordination ^f	5	4	3	7	4	8
Resource selection functions ^g	1	2	7	15	33	43
Occupancy models	0	0	0	0	7	14
Ecological niche models	1	0	0	1	2	5
Other ^h	6	3	4	1	0	2

^a Small rodents, shrews, squirrels, lagomorphs, sengis, tenrecs.

^b Macropod and other medium-to-large marsupials, large rodents, armadillos, anteaters, pangolin, dolphins, primates.

^c Scats, tracks, direct observations made during systematic surveys.

^d Spool-and-line tracking, powder tracking, owl pellets, light-tagging (bats), acoustic surveys (bats), landowner surveys, and studies using giving-up densities (GUDs).

^e Analyses that compare numbers of records in used versus available categories, such as chi-square tests, *G*-tests, Mann–Whitney *U*-tests, *t*-tests, univariate and multivariate analysis of variance, compositional analysis (Aebischer et al. 1993).

^f Multivariate analyses such as principal components analysis, discriminant function analysis, canonical correlation analysis.

^g Analyses based on regression models such as logistic regression and generalized linear models, usually ranked by Akaike’s information criterion (AIC) or the Bayesian information criterion (BIC), resource selection ratios.

^h Descriptions of habitat use without comparisons to availability, for example, distributions along elevational gradients, or descriptions of roost, den, or foraging sites without a statistical analysis; one study in 2017 used landscape genetics.

improves, the variety of studied species increases, as does the variety of investigated questions. For example, advances in telemetry and use of cameras have greatly increased the number of studies conducted on carnivorans and ungulates (Table 1). GPS collars permit analyses of how cover types and landscape elements are used by quantifying movement rates and paths (e.g., Karelus et al. 2017). Cameras allow photographic documentation of multiple animals, are not as limited as traps in the variety of species that can be detected, and can operate continually for long intervals of time without needing to be checked (e.g., Astete et al. 2017). Acoustic monitoring of bats allows greater ease of determining activity in different environments (e.g., Braun de Torrez et al. 2018). Because bats in flight often move too quickly to be tracked using hand-held antennae, and the number of bats that could be tracked was greatly limited, most early studies of habitat selection by bats involved selection of roost sites or hibernacula.

Sources for environmental and climatic data are now readily available at spatial scales previously inconceivable, and analytical methods are much more sophisticated. Remotely sensed data (e.g., satellite imagery and aerial videography) can be incorporated into geographic information systems (GIS), along with other environmental “layers” such as maps of waterways, cover types, roads and other anthropogenic features, photosynthetic activity, and climate, to permit analyses of landscape-level features and patterns. Whereas only two of 38 studies published from 1988 to 1997 (Table 1) obtained habitat availability data from such sources, 100 of 158 studies published from 2008 to 2017 did so. Advances in computer hardware and software have facilitated the implementation of intensive new methods of data analysis. The field has advanced from simple descriptions of habitat use and use of simple statistics to analyses based on resource selection functions, logistic regression, and Akaike’s information criterion (Manly et al. 2002).

Milestones regarding data analysis during the past 30 years include the development of compositional analysis (Aebischer et al. 1993), which uses individual animals as sampling units and compares their proportional use of various environmental features or cover types to those available in that animal’s home range (third-order habitat selection—Johnson 1980) or to a larger study area (second-order habitat selection); occupancy modeling (MacKenzie et al. 2006), which uses multiple surveys to estimate the probability of a species being present at a location after accounting for imperfect detection, and can be used to assess habitat selection when environmental covariates are included in predictive models; and ecological niche modeling (ENM), such as Maxent (Phillips et al. 2006), which relates records of species occurrence to ecological and climatic characteristics (“background”) to represent species distributions in ecological space. ENM can be used to generate maps that predict environmental suitability for a species, which may be extrapolated to larger geographic areas (Ribeiro et al. 2018). Such maps have become common in systematics and biogeography (Hoisington-Lopez et al. 2012; Gutiérrez et al. 2014). They can be particularly useful for conservation, as they can suggest areas suitable to survey for rare species of conservation

concern (e.g., Gerstner et al. 2018), or identify regions that might be conservation priorities for a species (Espinosa et al. 2018). ENM built on climate data can help predict range expansions or contractions that might occur under different climate-change scenarios (e.g., Baltensperger et al. 2017).

General principles.—Given the great strides in methods of data collection, availability of large-scale databases and GIS layers, and ability to conduct sophisticated computer-intensive analyses, a few general principles are now well established.

1) Habitat selection follows a hierarchical pattern that occurs across multiple spatial scales.—In a highly cited paper, Johnson (1980:69) defined a “natural ordering of selection processes”: first-order selection is the selection of a physical or geographic range of a species, whereas second-order selection determines the location of the home range of an individual within that range, and third-order selection reflects the use of environmental components within the home range. ENM typically describes first-order selection. Most studies of radio-tracked individuals describe third- or second-order selection, or both. Johnson (1980) also defines fourth-order selection as the procurement of food items from feeding sites. For mammals, examples include factors associated with kill sites of African lions (*P. leo*—Davidson et al. 2012) and browsing on different parts of *Acacia* trees by African ungulates (du Toit 1990).

2) Habitat selection can be affected by the configuration of cover types and landscape elements, not just their spatial extents.—As the consequences of habitat loss, fragmentation, and isolation received greater attention, it became clear that the amounts of available cover types were only one factor affecting selection (Presley et al. 2019). The size and shape of patches (i.e., areas of a particular cover type), the extent and types of edges between patches, connectedness among patches, the hostility of the surrounding (i.e., nonhabitat) matrix, and distances from various influences (e.g., anthropogenic disturbances) are examples of landscape-level factors now routinely included in analyses of habitat selection.

Studies of landscape ecology often describe relationships between species occurrence at a selected point, and variables measured at “local” (within a small buffer around the point), “patch” (relating to a generally homogeneous area within which the point occurs), and “landscape” (within a buffer that extends well beyond the immediate vicinity of the point) spatial scales. Statistical relationships between species occurrences and one or more variables at different scales are almost inevitably reported, demonstrating that animals select habitat based not only on the environmental characteristics of a particular site, but on a larger context in which that site occurs. One problem with this approach is that, unlike the orders of selection of Johnson (1980), a biological context for the scales examined is not always clearly defined. The local scale should reflect an animal’s perceptual range, but how are the larger scales determined? Buffer size is sometimes related to an average home range diameter or an average daily movement distance, but assessing availability of environmental variables within this area may not be straightforward; territoriality by neighboring individuals or groups may make some areas within the buffer off limits to the

focal individual, for example, or barriers to movements may inhibit accessibility. In studies involving the least amount of a priori biological knowledge, a range of buffers is used and researchers let the statistics suggest the scales at which selection is influenced. These exploratory analyses may suggest hypotheses for further study, but a mechanism underlying the observed relationships is speculative at best.

3) Habitat selection can be affected by individual sex, age, and reproductive condition.—Caution must be applied when making inferences from studies of habitat selection that do not identify individuals, but carefully designed studies can use such individual attributes to advantage. For example, the finding that subadult European pine martens (*Martes martes*) are overrepresented in areas of fragmented forest compared to adult-dominated, intact forest supports the hypothesis that forest fragmentation results in poorer-quality habitat for this species (Mergey et al. 2011). Analyses of habitat selection have been used effectively to investigate ecological and social interactions underlying sexual segregation in ruminant ungulates (reviewed in Main et al. 1996; Bowyer 2004). By describing alternative hypotheses, associated with clear predictions based on the timing of spatial segregation and the types of selected cover and forage, Ahmad et al. (2018) evaluated factors influencing sexual segregation in markhor (*Capra falconeri*). Reproductive stage affects habitat selection by many female mammals that must behaviorally accommodate energetic demands during reproduction and minimize predation risk for their offspring (e.g., Long et al. 2009). Age or social status may also influence habitat selection, sometimes with compelling fitness correlates. Snowshoe hares (*Lepus americanus*) exhibit risk-sensitive foraging, avoiding open areas even when food is available there. Young animals, however, may be forced to use these riskier habitats, where they are differentially preyed upon by great horned owls (Rohner and Krebs 1996). Clearly, interpretation of habitat selection should be limited to the time when that selection is measured.

4) Habitat selection expands with population density.—As population density increases, per capita fitness in a selected cover type likely declines, and eventually may equal per capita fitness in a previously unselected cover type. Thus, at higher density, individuals should assort themselves over a greater number of cover types so that fitness is equivalent in all occupied types (i.e., the ideal-free distribution of Fretwell and Lucas 1969). In an alternative model, the ideal-despotic distribution (Fretwell and Lucas 1969), subordinate individuals are constrained in their choices by dominant individuals who preempt areas with the best resources, such that fitness is unequal among cover types, although the number of cover types used still increases with density. Species that undergo dramatic population cycles (e.g., voles and lemmings) may occupy a limited number of “core” vegetation types at low densities but expand into “marginal” vegetation types during population increases (e.g., Sundell et al. 2012). Most mammals show some form of spacing behavior, and ideal despotic distributions are the most commonly observed pattern (e.g., Beckmann and Berger 2003).

5) Habitat selection can be affected by interactions with competitors and predators.—Differences in habitat selection in the presence or absence of another species with similar resource use is one of the standards by which the hypothesis of competition has been evaluated (see “Intraspecific Competition” and “Interspecific Competition” sections). The presence or abundance of putative competitors can be included as a covariate in analyses of habitat selection, particularly in camera-trap studies, where photos of multiple species at the same location are possible. The inclusion of potential competitors as covariates provides insight into community interactions, but these studies are primarily correlative. A hypothesis of competition may be supported by a pattern of negative spatial or temporal correlation, but cannot be concluded without replication and controls.

Predators can create a “landscape of fear” in which prey species experience habitat-specific levels of predation risk, causing prey to select areas that reduce predation risk even if reducing quality or availability of food resources. One well-studied but controversial example is the reintroduction of gray wolves to Yellowstone National Park in the United States, which resulted in elk altering habitat selection to reduce predation risk, such that riparian areas recovered from browsing, and initiating a trophic cascade (reviewed by Boyce 2018). Hartebeest (*Alcelaphus buselaphus*) select open areas and avoid areas near dense tree cover where African lions, an ambush predator, occur (Ng’weno et al. 2017). GUDs can provide insights into how different areas are used for foraging, and can reveal complexities of predator–prey interactions that are not apparent from presence-absence data. Makin et al. (2018) used GUDs from different cover types and at different proximities to dense vegetation to reveal species-specific responses of prey to the reintroduction of wild dogs in a reserve in South Africa.

Not all interspecific interactions are negative (see “Mutualisms” section). Conspecific attraction, the tendency of individuals to settle near conspecifics, is an understudied interaction that can affect habitat selection (Campomizzi et al. 2008). Conspecific attraction can result in spatial clustering of individuals, and can contribute to uncolonized patches of high-quality habitat if social cues that attract dispersers are absent. Many species of mammals, such as group-forming ground squirrels and species that aggregate at certain times of year (e.g., winter—Hays and Lidicker 2000), warrant investigation in this regard.

6) Presence-absence data and density are insufficient to measure habitat quality.—Knowing if a set of environmental conditions is sufficient for an individual to occur is insufficient for conservation or management of a species. The critical questions are how survival, reproduction, individual condition, and population persistence vary with different patterns of habitat selection, and how this interacts with population density. Effects of social status and population density on habitat selection suggest that low-quality cover types may be widely and even densely occupied at certain times. Many studies suggest that presence-absence and density are insufficient to measure habitat quality (reviewed in Rodewald 2015).

Areas included in studies of habitat selection can vary in quality over time. Certain resources may only become available seasonally, or may only be required at particular times of year, and selection of those areas may be undetected in short-term studies. Moreover, areas may vary from year to year in the availability of resources (e.g., fruit, seeds, or preferred vegetation that respond to weather; prey populations that fluctuate in abundance). For example, a forest type considered to be higher quality for North American red squirrels (*Tamiasciurus hudsonicus*) because of higher population densities can, during times of cone failure, become poorer-quality habitat relative to other forest types (Wheatley et al. 2002). The higher-density populations showed lower survival and reproduction, and higher turnover and immigration rates during a year of cone failure, and forest types with lower but more stable resource levels assumed greater importance for population persistence. Studies attempting to identify critical habitat for conservation should not stop after statistically demonstrating selection, but should seek to determine the underlying biological relationships that generate selection.

Critiques.—The proliferation of studies addressing habitat selection has led to an improved understanding of patterns across mammalian taxa. However, many studies remain limited in their spatial or temporal extent, and some contain or repeat flaws that call for further attention. We highlight three such issues that require renewed attention.

1) Most habitat selection studies are snapshots in space and time.—Most analyses of habitat selection describe behavior at a particular place by individuals with a history of experience in that place; inferences about the generality of the documented selection should be made with caution. First, availability of cover types and environmental characteristics differ between studies. Consequently, selective regimes likely vary among sites and may reflect different availabilities of a cover type more than actual differences in selective behavior (e.g., Di Blanco et al. 2017). For example, selection of a particular cover type may appear much stronger in a highly fragmented or degraded landscape compared to a landscape where that cover type is dominant (e.g., Spirito et al. 2017). Second, the mechanisms and fitness consequences associated with empirical patterns of resource selection are generally unknown. Thus, patterns at one site may reflect availability more than limits on species presence. For example, characteristics of tree cavities selected as roost sites by bats can differ among sites depending on the range of available options (e.g., Loeb 2017). Third, extrapolation into the future can be risky. The constraints on species adaptation to environmental change are speculative. For example, several species of carnivorans now occupy urban and suburban areas that they avoided initially (e.g., Gehrt et al. 2010).

2) Reliance on statistics to do our thinking can lead to mundane or confirmatory findings.—Some studies start with a weak justification such as “little is known about” habitat selection by a species of conservation interest. Researchers proceed to collect an impressive number of occurrence records, extract extensive data on the usual generic and predictable characteristics from online and other resources, use a variety of sophisticated

statistical analyses to measure selection, and conclude by speculating about cause and effect (see Morrison 2012 for a well-articulated discussion of this problem with studies of habitat selection). In spite of rigorous attention to methods of data collection and analyses, results of such studies are exploratory and generally should be considered hypothesis-generating rather than hypothesis-testing. Many studies offer conclusions such as selection of a broad cover type (e.g., forest) and negative association with anthropogenic disturbance or positive association with water, which are predictable rather than novel. Studies that use a procedure such as Akaike’s information criterion to rank large numbers of models that comprise different combinations of characteristics or spatial scales, and let the statistics determine what is “selected,” should instead design definitive studies or experiments that test particular a priori hypotheses of conservation concern.

3) Habitat selection studies intended “to inform conservation” need to dig deeper.—First, species that select broad environmental categories such as cover types (e.g., forest) are probably selecting particular things within them (e.g., McCann et al. 2014). Identifying the selected resources, whether they are structural features or food, can help determine how and why certain cover types are used, and thus where to focus conservation efforts or predict types of disturbance that will have the most severe negative impacts. Second, fitness consequences of habitat selection are rarely evaluated reliably. Assessing differences in mortality risk, reproductive success, and individual condition associated with patterns of habitat selection provide more useful insights for conservation than documenting presence. Third, population-level implications of habitat selection are the ultimate concern for conservation: how do patterns of habitat selection relate to population size, dynamics, and persistence? How these population characteristics, along with demography and genetics, vary across different landscapes can reveal relationships between habitat selection and population viability. To assist in development of meaningful conservation strategies, studies of habitat selection need to explore more than correlations between cover types or landscape elements and species presence. These are challenging goals, but if studies of habitat selection are to inform conservation or management, they must focus on information that is required for these goals (Morris 2003a), and design analyses to that end.

POPULATION DYNAMICS

Advances in Population Estimation

Understanding mammalian population dynamics relies heavily on the ability to collect data on individuals and populations, as well as on analytical techniques to estimate population parameters. Recent technologies, from camera traps and acoustic recorders to noninvasive genetics to drones, are providing much larger quantities of data than traditional observer-based methods. Concurrent with these developments in survey methodologies, advances in computer technology have greatly increased the capacity to process large amounts of data in reasonable amounts of time. Finally, new software packages such as the

open-source software R (R Core Team 2016) provide useful tools for the development of novel techniques.

This combination of novel data sources, easily accessible computer power, and open access software has stimulated the development of novel analytical methods. We focus on advances in statistical modeling for estimating population parameters relevant to the study of mammals. Most of these models confront the problem that efforts to enumerate individuals (or species) inevitably miss some fraction of those that are present, because many animals are shy, cryptic, or elusive, and range over large areas.

Advances in traditional techniques to estimate population parameters.—Perhaps the most fundamental objective of population ecologists is determining how many animals are in a population. Two traditional approaches to this involve live-trapping efforts, in which we capture and mark as many animals as possible, and then use the frequency (and pattern) of recaptures to determine how many animals are present; and distance sampling, in which we conduct surveys to determine the spatial distribution of animals (relative to a point or transect) and then determine the effective area of sampling to estimate density. Both of these approaches have been subject to substantial improvement in recent decades.

1) Capture-recapture.—Capture-recapture (CR) models have a long tradition in mammalian population ecology as the gold standard for estimating demographic parameters such as population size and density, survival, or recruitment. They require repeated detections of individually recognizable animals to estimate the probability that an individual is detected, given that it is present. They then produce estimates of the demographic parameters of interest while correcting for imperfect detection. These models can be divided into closed population models, which assume no loss or gain in individuals over the course of the study and focus on estimating abundance and density, and open population models, which estimate dynamic parameters such as survival and recruitment. Much of the groundbreaking development of CR models took place in the 20th century (Otis et al. 1978; Pollock et al. 1990), spurring a wealth of CR studies.

An important area of ongoing CR model development concerns multistate models. These models were originally developed to allow individuals to move between sites (i.e., spatial states—Schwarz et al. 1993), but were quickly generalized to other types of “states,” such as age class or breeding status (Nichols et al. 1992, 1994). Estimates of state transition probabilities, such as transition from one site to another, are of great interest in basic and applied population ecology, for example, when estimating the contribution of subpopulations to meta-population growth (Nichols et al. 2000a).

Capture-recapture methods have seen increased application in large mammal population studies due to the emergence of camera-trapping and noninvasive genetic sampling. The combination of CR with these field techniques has made it possible to monitor populations and obtain estimates of vital rates for large mammals that would be prohibitively difficult and dangerous to capture repeatedly (e.g., tigers [*P. tigris*]—Karanth et al. 2006).

Other CR advances (reviewed by Frederiksen et al. 2014) range from accounting for misidentification (Lukacs and Burnham 2005; Yoshizaki et al. 2009) to modeling abundance-habitat relationships in spatially structured closed populations (Converse and Royle 2012). In addition, spatial capture-recapture (SCR—Efford 2004; Royle et al. 2014; discussed in Novel frameworks for estimating population parameters) has emerged as a novel framework that takes into account how the juxtaposition of individual home ranges with sampling effort affects detection probability and density estimation.

2) Distance sampling.—Distance sampling (Anderson and Pospahala 1970) is a form of transect sampling, which assumes that the probability of detecting an animal declines with its distance from a transect line or point. By fitting a detection function to observed distances, detection probability and, by extension, abundance can be estimated.

The distance sampling framework allows for detection functions with different shapes (Burnham et al. 1980). More recently, models have been extended to allow for covariates such as habitat, observer skill, or climate to explain variation in detection probability (Marques and Buckland 2003). Model development has targeted relaxing a core assumption of distance sampling, that detection on the transect line is perfect (Borchers et al. 1998, 2006).

Applications of early “conventional” distance sampling were based on data pooled across multiple transects, thereby precluding investigation of relationships between density and covariates such as habitat measured at the sampling unit scale. Multiple recent methods allow investigation of this relationship, either by fitting general additive models to sampling unit-specific estimates of density (e.g., density surface modeling—Miller et al. 2013), by integrating estimation of abundance across sampling units as a function of covariates (Royle et al. 2004), or by using spatial point process models (models that describe the distribution of points in a spatial domain—Niemi and Fernández 2010; Conn et al. 2012).

Other modifications include models that allow for temporary emigration from a survey strip or plot, particularly important for mobile animals (Chandler et al. 2011), and imperfect availability for detection (Borchers et al. 2013), modifications that are useful for species like cetaceans that spend considerable time invisible to the observer. Distance sampling has been expanded to accommodate analysis of multiple species in a community-model framework (Sollmann et al. 2016), which improves parameter estimates for rare species by “borrowing information” from more abundant species (Dorazio and Royle 2005; Dorazio et al. 2006), and estimation of survival and recruitment from multiple years of distance sampling data, using a state-space modeling approach (Sollmann et al. 2015).

Novel frameworks for estimating population parameters.—Recent years have seen substantial development of novel approaches for estimating population parameters. These include expanding traditional CR methods to account for the spatial distribution of animals relative to sampling effort; novel means of estimating abundance from unmarked populations; development and application of occupancy modeling

to temporal dynamics, distinct trait states, and patterns of species co-occurrence; and integrated population models (IPMs), which allow researchers to combine some of these techniques to capitalize on the strengths and output of each.

1) Spatial capture-recapture.—Traditional closed population CR methods produce estimates of abundance, but density is frequently a more useful measure to compare populations among sites or surveys. Highly mobile animals are bound to use areas beyond the immediate area covered by sampling effort, and the difficulty in determining this effective sampled area has long been recognized (Bondrup-Nielsen 1983; Wilson and Anderson 1985). The extent to which individual home ranges overlap with sampling efforts also influences the probability that individuals will be detected, a source of heterogeneity in detection probability that cannot be addressed mechanistically in traditional CR approaches.

Spatial capture-recapture (Efford 2004; Borchers and Efford 2008; Royle et al. 2014) uses capture locations to account for animal movement and individual home range overlap with sampling effort when estimating detection probabilities. By modeling the location of individual home ranges as a spatial point process, density in SCR is defined as the number of individuals in the spatial domain of the point process divided by its area. The SCR framework can readily be extended to incorporate multiple spatial processes of interest. Density within the spatial domain can be modeled as a function of environmental covariates (Borchers and Efford 2008). Resource selection functions can be incorporated to allow animals to use different habitats with different intensity (Royle et al. 2013). Models can make use of resistance surfaces to adequately reflect individual movement across the landscape (Sutherland et al. 2015). SCR models can be extended to open populations (Gardner et al. 2018) and mark-resight surveys (Sollmann et al. 2013), but these advancements are not yet fully generalized. Finally, SCR allows for more flexible study designs (smaller trap arrays, uneven coverage by traps) compared to traditional CR (Sollmann et al. 2012; Efford and Fewster 2013), which is especially beneficial for the study of wide-ranging species. As a consequence, the use of SCR in the study of animal populations has increased dramatically since the framework's inception (Royle et al. 2014).

2) Estimating abundance from unmarked populations.—Whereas CR methods require repeated detections of individuals, another class of approaches to abundance estimation is based on counts of individuals, and is much less effort-intensive. With certain survey protocols such as double-observer (Nichols et al. 2000b), removal (Farnsworth et al. 2002), or N-mixture models (Royle 2004), counts can be used to account for imperfect detection. These methods are most frequently used to estimate abundance in birds (Royle 2004), which generally are easier to count by direct observation compared to mammals, and are thus not discussed in detail. However, applications of these methods to mammals include removal sampling for bats (Duchamp et al. 2006), N-mixture modeling of camera-trap data (Brodie and Giordano 2013; Froese et al. 2015), and call-in survey data of African lions (Belant et al. 2016).

Whereas the abovementioned count-based methods rely on spatially independent survey locations, Chandler and Royle (2013) developed a model that makes use of the spatial correlation in counts across closely spaced detectors to estimate animal density (essentially an SCR model without individual identification). Density estimates from this model are very sensitive to study design, and it has not yet been widely applied (but see Jiménez et al. 2017 for an application to camera-trapping data).

Finally, Rowcliffe et al. (2008) developed a model for camera-trapping data that is based on an ideal gas model and estimates density as a function of animal movement speed, the area of the detection zone of the camera, and encounter rates between animals and traps. The model assumes random movement of individuals, requires that camera traps are deployed randomly with respect to animal movement, and knowledge of, or the ability to estimate, movement speed and the amount of time individuals are active. This approach has been used for several mammal species, including African lions and European pine marten (Manzo et al. 2012; Cusack et al. 2015), and was recently expanded to accommodate acoustic detection of bats (Lucas et al. 2015).

3) Occupancy modeling.—Species occurrence is an alternative state variable to abundance that allows researchers to describe species distributions and habitat associations. However, detecting a species at a site potentially suffers from the same difficulties as detecting an individual in a population—we may fail to detect it despite its presence. The framework of occupancy modeling, developed by MacKenzie et al. (2002, 2006), uses repeated species detection/nondetection surveys to estimate the probability of species occurrence while accounting for imperfect species detection. Occupancy models are widely used across many taxa because of the (relative) ease with which species-level detections can be obtained (compared to individual-level data or counts).

Occupancy models were developed for application with discrete habitat patches, but they are frequently applied to point-sample data collected in continuous habitats. Specifically for mammals, they are often used to analyze camera-trapping data (e.g., Rich et al. 2016), and results typically are interpreted in terms of habitat use rather than occurrence (MacKenzie and Royle 2005). This has been criticized because of the difficulties of defining the size of a plot to which occupancy applies, and because depending on plot size, occupancy is confounded with density and home range size, and may therefore not be comparable across surveys or species (Efford and Dawson 2012).

Occupancy modeling has been extended in multiple ways, many of which have been applied to mammals. Multiple-season occupancy models allow estimation of patch extinction and colonization (MacKenzie et al. 2003), parameters that can be used to describe metapopulation dynamics (Sutherland et al. 2014). Multistate models go beyond incidence and allow inclusion of states such as absent, present, and breeding (Nichols et al. 2007). The Royle–Nichols model (Royle and Nichols 2003) links species detection probability to abundance (where there are more individuals of a species, we have a higher probability of detecting at least one individual) and allows estimation

of local abundance from detection/nondetection data. Two-species occupancy models allow investigation of patterns of co-occurrence and avoidance (MacKenzie et al. 2004), whereas community occupancy models (Dorazio and Royle 2005; Dorazio et al. 2006), implemented in a Bayesian framework, have been used to estimate species richness at multiple spatial scales (Tenan et al. 2017).

4) Integrated population models.—Traditionally, population monitoring programs and ecological studies have used separate analyses of different types of data to quantify different population parameters. In contrast, IPMs combine some of the previous techniques to analyze multiple data types and simultaneously estimate multiple demographic parameters. These models involve the joint modeling of data on population size (often count-based surveys) to estimate abundance, and demographic data (generally CR data) to estimate dynamic parameters such as survival (Besbeas et al. 2002; Schaub and Abadi 2011). The approach draws on the fact that both types of data contain information about dynamic population parameters because demographic parameters underlie changes in abundance over time. Combining such data can facilitate estimation of demographic parameters that cannot be estimated from either data source alone. For example, combining count data with mark-resighting data allows estimating abundance (from counts), survival (from mark-resighting data), and recruitment, which cannot be estimated from counts or mark-resighting data alone (Besbeas et al. 2002).

Intraspecific Competition

Competition has been a dominant theme throughout the history of ecology, and is an essential mechanism underlying much of natural selection. Intraspecific competition takes many forms and may be more common and significant than interspecific competition (Jiang et al. 2015). Intraspecific competition implies density-dependence (DD) and this is essential to logistic growth and considerations of carrying capacities and resource limitation. Most studies in recent decades have quantified DD as a means of understanding foraging ecology, behavioral ecology, or demography.

Characterizing competition.—One approach to assess the strength of intraspecific competition is to experimentally manipulate population density and quantify a measurable parameter related to competition. For example, under experimental conditions, male Allenby's gerbils (*Gerbillus andersoni allenbyi*) interfere with foraging by females, leading to temporal shifts in activity by the latter (Mitchell et al. 1990; Kotler et al. 2005). Intraspecific competition between pairs of Allenby's gerbils reduces individual foraging success by over 50% (such that single animals harvested more food than the combined efforts of two Allenby's gerbils—Berger-Tal et al. 2015). This was explained in the context of the Tragedy of the Commons, in which individual investment in competition leads to reduced foraging success by all individuals.

Capture-mark-recapture studies have also played key roles in testing for competition, either comparing fitness parameters at sites with different population densities or with different levels

of resource availability. One such study (Lobo and Millar 2013) demonstrated that supplemental food (spruce seeds) improves overwinter survival in deer mice (*Peromyscus maniculatus*) in boreal forests, although this did not extend to natural spruce masting events when deer mice competed with North American red squirrels, a dominant pre-dispersal predator of spruce seeds.

Marino et al. (2014) applied distance sampling methods to compare recruitment in guanaco (*Lama guanicoe*) populations in two predator-free reserves. One population grew from low to medium density (ca. 4–26 animals per km²), while the other grew from medium to high density (ca. 46–71 animals per km²). Recruitment was similar at both sites, but more variable at the high-density site. Model selection indicated that this variation was positively influenced by forage availability at both sites, whereas recruitment per se was depressed by population density only at the high-density site.

Most studies assessing intraspecific competition in wild populations have relied on time-series analyses to characterize direct and delayed DD within species, and explaining residual variation with environmental correlates. The power of such analyses clearly increases as time series lengthen, but maintaining comprehensive sampling regimes over such periods is financially and logistically challenging (Schrader and Hayes 2017; Kuebbing et al. 2018).

Time series may be characterized with general linear models (usually complemented with general additive models to confirm the assumption of linearity). Comparison of competing models allows determination of which a priori sets of parameters most parsimoniously explain the observed patterns. A second linear approach, increasingly common, applies autoregressive models to time series to determine the “order” of demographic feedback (Royama 1992; see also Bjornstad et al. 1995; Berryman 1999; Turchin 2003; see also “Population Cycles” section). First-order feedback reflects direct DD, whereas higher-order feedback reflects delayed DD at various time lags. Although many assume linearity in modeling, this approach has limitations (e.g., Bjornstad et al. 1995). Nonlinear approaches may also be used with autoregressive models, generally by assessing serial autoregressive models across one or more thresholds (e.g., Stenseth et al. 1998).

Within the Royama framework, many mammals are characterized by second-order autoregressive models, the characteristics of which vary greatly with the strength of direct and delayed DD. However, the relative influence of density-independent (DI) factors also may vary across climatic gradients. Autoregressive models clarified that both DD and DI factors influence demographic patterns of red deer (*C. elaphus*) in Norway (Forchhammer et al. 1998); moreover, both DD and DI influences operated through direct (principally through mortality of both sexes) and delayed (via growth and fecundity among females) pathways. Imperio et al. (2012) applied GLMs to a population of red deer in Italy, where DD was the dominant factor influencing population growth rate, but as expected for a system with a relatively benign climate, the influence of DI factors was less. Similarly, Post (2005) suggested a gradient in the strength of direct DD in 27 populations of woodland caribou

(*Rangifer tarandus caribou*), with DD declining toward northern latitudes.

Darwin's leaf-eared mouse (*Phyllotis darwini*) displays very different dynamics at two national parks in Chile. At an interior site, this species shows clear signs of both direct (e.g., intraspecific) and delayed (likely due to predation by barn owls, *Tyto alba*) regulation (e.g., Lima and Jaksic 1998). In contrast, only first-order dynamics were demonstrable at a coastal site, with no indication of a significant role of predation (Previtali et al. 2009). This may reflect the relative stability of resource dynamics at the latter site, where coastal fog provides more consistent moisture for vegetative growth, such that competition for food remains a dominant influence, even in rainy years.

These examples underscore the challenges of extrapolating too broadly with data from a single site, as has been shown in geographic gradients in DD among arvicoline rodents (Bjornstad et al. 1995; Stenseth et al. 1996) and some ungulates (Post 2005). In a third approach, Lande et al. (2002, 2006) estimated DD across the entire life history of age-structured populations. This requires more comprehensive data than does simpler linear modeling, and consequently has seen limited use. Simard et al. (2012) applied linear and autoregressive modeling as well as Lande-style analyses to evaluate DD in white-tailed deer in Quebec. Their understanding of the life history of this population led the authors to expect both direct and delayed DD, but neither linear nor autoregressive models supported this. In contrast, Lande's approach provided strong evidence for DD, suggesting that multiple tests for DD should be pursued where possible (see also Forchhammer et al. 1998).

Competition influences vital rates.—Population density may depress condition, winter survival, and fecundity in ungulates (Stewart et al. 2005; Mobaek et al. 2013). Density-dependent mechanisms reduce condition and fecundity of elk more than do DI factors such as precipitation and temperature (Stewart et al. 2005). White-tailed deer adjust life-history strategies under DD, maintaining reproductive output at the expense of growth (Simard et al. 2008). Some mammal species exhibit "competitive growth" in the face of rapidly growing same-sex conspecifics (Huchard et al. 2016); meerkats (*Suricata suricatta*) even increase food intake and growth rates when same-sex rivals increase their growth rate.

Competition influences home range size and habitat selection.—Home ranges of many species are inversely related to population density (e.g., Drake et al. 2015), although not always (Kilpatrick et al. 2001). For social species, group size may represent a trade-off between competing costs. Home ranges of yellow baboons (*Papio cynocephalus*) are larger for small and large groups than for intermediate-sized groups, reflecting a transition from socially subordinate and smaller groups that are constrained by intergroup competition as well as by predation, to socially dominant and larger groups that are constrained by intragroup competition (Markham et al. 2015). For several species, group size represents a balance between scramble competition within groups, and contest competition between groups (Kurihara and Hanya 2015).

Animals should select a restricted range of more preferred habitat at low population densities, and become more opportunistic as densities increase, and favored habitat is less available (Fretwell and Lucas 1969; Rosenzweig 1981). Numerous mammals have exemplified such dynamic habitat use and selection (e.g., rodents—Morris 2003b; ungulates—McLoughlin et al. 2006; Morris and MacEachern 2010; Pérez-Barbería et al. 2013; lagomorphs—Kawaguchi and Desrochers 2018).

Competition may lead to individual specialization.—Numerous studies illustrate individual dietary specialization among mammals (Araújo et al. 2011). A key issue is whether this reflects availability of resources or a response to competition for limited resources. Three examples appear to support a competitive mechanism. Darimont et al. (2009) attribute variation in carbon and nitrogen stable isotopes among gray wolves from islands off British Columbia to local depression in the availability of terrestrial herbivores (mule deer, *O. hemionus*) such that intraspecific competition leads to increased consumption of marine resources. In the Alaska Range, the preferred prey of coyote (*C. latrans*) is snowshoe hare, but when hare numbers declined, and intraspecific competition presumably increased, different individual coyotes favored different alternative prey, such that population niche width increased and diet overlap remained constant (Prugh et al. 2008). Finally, sea otters in food-limited environments exhibited greater individual dietary specialization than those in food-rich environments (Tinker et al. 2008), and individual specialization is greater at sites with rocky substrates than mixed substrates (Newsome et al. 2015), suggesting an interaction between competition and environmental influences.

Source and Sink Dynamics

Traditional approaches in population ecology considered populations as single, homogeneous collections of individuals in arbitrarily defined spaces. Based on this view, ecologists sought to understand populations by analyzing time series of either total abundance or life-history rates, along with underlying DD and DI factors, and associated sources of uncertainty (Gotelli 1998). These approaches ignore ubiquitous spatial heterogeneity in populations (Akçakaya 2000). Ecologists and conservation biologists have increasingly relied on spatially explicit consideration of population dynamics, taking into account spatial heterogeneity and dispersal among local populations to understand the dynamics and conservation needs of populations (Kareiva 1990).

Spatial heterogeneity in population structure is caused by external factors such as naturally or anthropogenically fragmented habitats, internal factors such as the territorial behavior of solitary individuals, family groups, or extended social groups, or an interaction of external and internal factors. Spatial heterogeneity is an inherent characteristic of mammalian populations because territorial behavior in mammals structures the patchy distribution of local populations, while natal dispersal of young ensures exchange of individuals among local populations. The resulting regional population (i.e., metapopulation) is a dynamic network of local sources and sinks, where average

fitness differs over space and time. Accurate characterization of these sources and sinks—and associated fitness—is important for understanding how the long-term persistence of a focal population depends on the rest of the metapopulation, and how metapopulation persistence, in turn, depends on each focal population.

Traditional metapopulation models (e.g., Hanski 1999) assume that regional population dynamics are driven by local extinction and recolonization events in habitat patches of similar quality. In contrast, source–sink models are based on the assumptions that 1) habitat patches differ in quality, 2) high-quality patches (sources) produce a surplus of individuals while low-quality patches (sinks) run a deficit, 3) populations in source habitat are regulated by DD processes, and 4) populations in sink habitat are sustained by dispersers from source habitat (Diffendorfer 1998). In addition, dispersal usually is assumed to be constrained.

Dispersal is central to source–sink dynamics.—The ability of species to disperse between habitat patches and to recolonize patches where subpopulations have gone extinct is a key factor driving the dynamics of spatially structured populations in general, and source–sink dynamics in particular (Kendall et al. 2000). Practical and technological constraints, however, have limited empirical work to local populations and precluded study of the complexity in between-population processes, particularly in dispersal of individuals (Nathan 2001). As a result, understanding of demography and evolution of spatially structured populations draws mainly on a few established local populations and remains largely uninformed with respect to dispersal.

To understand the causes and eco-evolutionary consequences of dispersal, Bowler and Benton (2005) call for research to investigate three substages of the dispersal process: 1) the pre-dispersal phase leading to emigration, 2) the transient phase, during which individuals search for a new patch outside their home range, and 3) the settlement phase. Each stage can be DD or DI, and can be driven by local (e.g., inbreeding avoidance, sibling competition, DD, conspecific attraction, and escaping imminent extinction) or regional (e.g., temporal and spatial variance in habitat quality, favorable conditions for migration—Hanski 1999) factors. For example, the decision to settle in a particular area may be affected by the characteristics of the area as well as by interactions between individual state (e.g., physiological condition) and environmental conditions (e.g., predation risk, climatic factors, population density, habitat quality) during the exploratory transient phase (Graf et al. 2007; Cote et al. 2013). These complex interactions may explain contrasting results on the effects of kin competition on dispersal (Guillaume and Perrin 2009; Purcell et al. 2012). Studies focusing only on a single stage of the dispersal process, for example, have reported support for (Bitume et al. 2013) and against (Hoogland 2013) the effect of kin competition on dispersal in social species.

For populations structured into social groups, the fitness of any individual is equivalent to the rate of increase of its descendant groups (Al-Khafaji et al. 2009). In such populations, in which individuals must disperse to form new groups, fitness is

directly tied to dispersal success. Many studies of social species have focused on proximate correlates of fitness, such as lifetime reproductive success, but few have taken the next step of assessing offspring dispersal success, and the processes that regulate settlement and reproductive success after settlement remain largely unknown (Nathan 2001). However, individual measures of fitness are only relevant in a population context (Wright 1930) and meaningful only relative to those of alternative strategies (i.e., to remain in the natal group and either contribute to inclusive fitness or wait for reproductive opportunities). Consequently, keeping track of individual dispersers—and viewing their fate in light of the fate of other individuals in the population—is necessary to understand selective benefits in structured populations.

Dispersal patterns and life-history characteristics relevant to dispersal are likely aligned along a continuum (Diffendorfer 1998). At one end are highly vagile species that are able to assess habitat quality; such species tend toward balanced dispersal among patches (e.g., small mammals). At the other end are species with low vagility or passive dispersal; these species tend toward source–sink dynamics (e.g., annual plants). In the case of attractive sinks (Delibes et al. 2001), however, active dispersers might be more tempted than passive dispersers to settle in sink patches. Such maladaptive behavior can arise if high mortality or breeding failure in attractive sinks is difficult to detect (e.g., due to human hunting or pollution), which, in turn, can severely affect the demography of populations in source habitats (Gundersen et al. 2001). Human activities can create attractive sinks so quickly that active dispersers might be unable to make optimal decisions. For example, an individual may select the same habitat as its predecessors, even if this choice no longer provides high fitness because habitat quality has degraded abruptly (Remeš 2000).

Identifying source and sink populations.—In a seminal paper, Pulliam (1988) suggested estimating four patch-specific demographic rates: birth (b), death (d), emigration (e), and immigration (i). Source populations were defined as local populations that produce a demographic surplus ($b > d$) and act as net exporters of individuals ($e > i$), whereas sink populations were defined as local populations that produce a demographic deficit ($b < d$) and act as net importers of individuals ($e < i$). These definitions, however, are only valid, if the regional population is at dynamic equilibrium (i.e., if $b + i - d - e = 0$ for all local populations). As an alternative, Runge et al. (2006) developed a method for differentiating sources and sinks that does not assume equilibrium conditions. They proposed a contribution metric (C^r), which measures the per-capita contribution of a local population to the regional population. C^r is calculated as the sum of the self-recruitment rate (i.e., local population growth rate minus immigration rate) and the successful emigration rate. If $C^r > 1$, the local population is a source; if $C^r < 1$, the local population is a sink.

Newby et al. (2013) show how the C^r method can be applied to natural populations. They estimated mean annual C^r during two periods in each of two cougar (*Puma concolor*) subpopulations, using long-term data on radiocollared individuals.

These populations were from the Northern Greater Yellowstone Ecosystem (NGYE) and the Garnet Mountains in Montana (GM). For the NGYE population, they distinguished periods before and after the reintroduction of wolves to the area; for the GM population, they distinguished periods before and after hunting was prohibited in the core area of the study site. They found that the NGYE population was most likely a source in both pre-wolf and wolf periods. Notably, the self-recruitment rate appeared to be too low to preserve the local population, but dispersal among subpopulations pushed the C^* value above unity, so that the NGYE population was a net contributor of individuals. In contrast, the GM population changed from a sink, when hunting was permitted in the core area, to a source once hunting was prohibited.

As an alternative to demographic studies, the source–sink status of populations may be inferred from studies of landscape genetics (Montgelard et al. 2014). DNA samples required for such studies have been obtained from live and dead individuals (yellow-rumped leaf-eared mouse, *Phyllotis xanthopygus*—Kim et al. 1998; cougar—Andreasen et al. 2012; black bear, *Ursus americanus*—Draheim et al. 2016; wild boar, *Sus scrofa*—Stillfried et al. 2017), from feces (woodland caribou—Ball et al. 2010), and from fossils (Uinta ground squirrel, *Spermophilus armatus*—O’Keefe et al. 2009). In the two earlier studies (Kim et al. 1998; O’Keefe et al. 2009), individuals were genotyped by analyzing segments of the mitochondrial cytochrome *b* gene; in the more recent studies, they were genotyped based on microsatellite loci.

Contribution of sinks to regional population persistence.—Using an offspring-allocation model, Jansen and Yoshimura (1998) investigated a two-patch scenario. In their model, the first patch was mostly of high (i.e., source) quality, but was occasionally struck by catastrophes that caused the local population to go extinct. This first patch therefore acted as a sink in the long term. The second patch was of constant low quality and acted as a sink at all times. Because both patches were functional sinks, given enough time, the regional population went extinct when offspring were allocated to just one of the two patches. When offspring were simultaneously allocated to both patches, however, the regional population survived. Persistence was possible because individuals from the low-quality (i.e., permanent sink) patch recolonized the high-quality patch after catastrophes had eliminated its local population.

The Alabama beach mouse (*P. polionotus ammobates*) provides an example that approaches the scenario modeled by Jansen and Yoshimura (1998). This mouse preferentially inhabits sandy dunes along the beachfront, but also occurs at low densities in the scrub-dominated area on the landward side of the dunes (Falcu and Danielson 2011). Dune habitat is of high quality, whereas scrub habitat is of low (potentially sink) quality, but the two habitats differ in vulnerability to hurricanes, which can completely destroy dunes, but usually leave the scrub areas intact. Mice finding shelter in these areas then start recolonizing the gradually recovering dune habitat. The recovery of dune habitat can be accelerated by erecting sand fences and by planting vegetation. Nonetheless, simulations

suggest that decelerating the decline of sink populations (e.g., through supplementary feeding) might be a better strategy to save populations than is the acceleration of recovery of source habitat (Falcu and Danielson 2011).

Anthropogenic sinks.—Humans can cause population sinks by modifying the landscape and through direct interactions with wildlife. Examples of the former include the building of roads through nature reserves (Kerley et al. 2002), the destruction and fragmentation of forests (Lampila et al. 2009), and urbanization (Hoffmann et al. 2003). Examples of direct interactions include management and malicious killing in human–wildlife conflict areas (Mace and Waller 1998), accidental killing (e.g., roadkill—Ramp and Ben-Ami 2006), and hunting (Robinson et al. 2008; Newby et al. 2013). Intense hunting can actually create population sinks in otherwise high-quality patches (Robinson et al. 2008) because animals, being unaware of the increased mortality risk in these “attractive sinks” (Delibes et al. 2001), may keep immigrating. Such behavior can even turn unhunted, but connected, source patches into sinks, if hunting pressures and dispersal rates are high (Gundersen et al. 2001). Finally, even interactions with good intent, such as the handling of individuals for monitoring purposes, can cause population sinks (Clinchy et al. 2001). Management-trapping of Yellowstone grizzly bears (*U. arctos*), for example, almost doubled the mortality rate, inducing a source–sink structure between bears that were never trapped and bears that were trapped at least once (Pease and Mattson 1999).

Anthropogenic sinks often arise from a combination of several activities. The Iberian lynx (*Lynx pardinus*) population in the region of the Doñana National Park (southern Spain), for example, once suffered heavily from illegal trapping, road traffic, hunting with hounds, and accidental drowning in irrigation wells (Ferreras et al. 1992). This human-caused mortality created population sinks outside the protected park area, whereas source populations inside the park remained largely unaffected (Gaona et al. 1998). Owing to comprehensive conservation efforts, the Iberian lynx is currently recovering (Simón et al. 2012).

Extreme cases of anthropogenic sinks are “ecological traps” (Mills 2013:189). Ecological traps arise when modifications to the landscape break the correlation between habitat quality and cues used by animals to assess this quality (Schlaepfer et al. 2002). This mismatch between cue and quality can deceive individuals into preferring low-quality over high-quality patches (Battin 2004), although such preferences have rarely been demonstrated convincingly (Robertson and Hutto 2006). Florida manatees (*Trichechus manatus latirostris*), for example, either migrate south or seek refuge in natural warm springs or in heated power-plant effluents during winter (Shane 1984). In the latter refuge, they may experience increased mortality if power plants are shut down temporarily (Packard et al. 1989). This phenomenon has been repeatedly quoted as an example of an ecological trap (Schlaepfer et al. 2002; Cristescu et al. 2013), yet it remains unknown whether Florida manatees actually prefer industrial warm-water effluents—the presumed trap habitat—over natural warm-water sources (Robertson and Hutto 2006).

Conservation implications of source–sink dynamics.—From theoretical perspectives, both source and sink patches can be important for the long-term survival of populations. The benefits of source patches are obvious; in addition to being self-preserving, they sustain local populations in sink patches. Sink patches, on the other hand, can help to stabilize and rescue local populations in source patches, and may serve as stepping stones between patches during dispersal (Jansen and Yoshimura 1998; Furrer and Pasinelli 2016). Finally, even the inter-patch matrix is important for regional population dynamics, because the nature of this matrix affects, for example, survival rates and how fast dispersers move between patches, and thereby influences the connectivity among patches. These observations suggest that the entire landscape warrants preservation, and whereas visionary ecologists think at this scale (e.g., Watson and Venter 2017), such a comprehensive management strategy appears currently unrealizable. Consequently, correct assessment of the source–sink status of local populations is a prerequisite to conservation and management practices.

Several problems may constrain the applicability of source–sink theory to decision-making in conservation (Wiens and Van Horne 2011). First, measuring local demographic parameters is notoriously difficult, yet collecting this information is crucial for distinguishing sources from sinks. Second, although organisms typically inhabit highly complex environments, simple source–sink models usually do not account for environmental complexity such as the spatial configuration of patches and the connectivity among them. Ignoring this complexity might lead to inappropriate conservation decisions. Third, because the functional role of any patch can change over time, a single assessment of demographic rates or of patch quality can be misleading (Dias 1996). Finally, inferred population dynamics depend largely on the spatial and temporal scales of observation (cf. Levin 1992). Shifts in source–sink status, for example, can only be observed if local demographic parameters are measured over time (Wiens and Van Horne 2011). Measuring such parameters requires the delineation of patch boundaries, that is, the definition of what actually constitutes a local population. This definition, in turn, is affected by the spatial resolution of observation. Selecting appropriate spatial and temporal scales of observation are nontrivial tasks and depend largely on the study organism (Wiens and Van Horne 2011; Furrer and Pasinelli 2016). The study area, for example, should extend to at least the maximal dispersal distance known for individuals of the focal population(s); otherwise, dispersal success cannot be measured accurately.

The source–sink concept is useful for describing population dynamics within and around protected areas (cf. Iberian lynx). In the context of population management, the purpose of establishing protected areas is to create or preserve source habitat. That is, local populations within protected areas are expected to produce a surplus of individuals and to sustain local populations outside these areas. For some species, however, protected areas actually function as sinks and thereby invite a net influx of individuals (Hansen 2011). Such counterintuitive dynamics can arise if the biophysical conditions within the protected

areas are harsher than in the surroundings, an unfortunate scenario that is often a reality (Hansen 2011). Sink populations inside protected areas are an undesired outcome of conservation efforts, because the persistence of such populations depends on the presence of source populations in unprotected areas, unless intense selection enables evolutionary rescue. Yet even source populations inside protected areas can become vulnerable to extirpation if human activities in surrounding high-quality areas turn these latter areas into attractive sinks. In such cases, effective conservation interventions would be to expand protected areas or change human behavior (Hansen 2011).

Population Cycles

Periodic outbreaks in small mammal numbers have been observed throughout history and are of interest as a fundamental natural phenomenon, as well as being relevant to human health (e.g., plague). Charles Elton's pioneering work on mammalian ecology (Elton 1924, 1942) was motivated by a visit to Norway in 1923 where he learned about the spectacular rise in numbers of lemmings, and their sudden and regular disappearance (Chitty 1996). Thus, population cycles have been a foundational problem in population ecology, and these remain among the most important and unresolved issues in ecology (Stenseth 1999). Progress in our understanding has been reviewed periodically (e.g., Batzli 1992; Stenseth 1999; Krebs 2013). Because research on snowshoe hare cycles has recently been summarized elsewhere (Krebs et al. 2018), we focus attention here on cycles and cyclicity among arvicoline rodents.

Definitions of population cycles.—The most prominent feature of cyclic populations is multiannual fluctuations in abundance, with generally clear phases (increase, peak, decrease, and low) occurring at 3- to 5-year intervals (Krebs 2013). Statisticians and theoretical ecologists generally define cyclic populations in terms of the parameters of second-order log-linear autoregressive models, with the pattern and periodicity of population fluctuations determined by the relative magnitudes of first- and second-order autoregressive parameters (Royama 1992; Bjornstad et al. 1995; Stenseth 1999; Turchin 2003; see also “Intraspecific Competition” section). Another recent approach involves wavelet analysis (Brommer et al. 2010).

In contrast, empirical ecologists also consider phase-related changes in behavioral, physiological, and life-history traits, with implications for both survival and reproductive rates (Boonstra 1994; Krebs 1996, 2013). Together, this suite of changes constitutes the biological (as opposed to mathematical or statistical) definition of population cycles (Krebs 1996). At peak densities, the breeding season shortens, juvenile survival declines, and age at maturity and reproductive rates decline; concomitantly, the mean age of reproductive females, average body mass, and levels of aggression increase. Hypotheses attempting to explain population cycles must account for phase-specific changes in population characteristics, as well as broader spatial and temporal patterns in abundance (e.g., Oli 2003; Krebs 2013).

Potential explanations for rodent cycles may be placed in five broad categories based on causal factors—food, predation, disease, self-regulation, and multifactorial hypotheses—and

hypotheses to explain these have been organized under two general dichotomies (Batzli 1992). One dichotomy contrasts the intrinsic school, which posits that factors such as genetics, dispersal, social behavior, and stress response are necessary and sufficient to cause population cycles (e.g., Chitty 1960), with the extrinsic school, which argues for control by factors such as food, predators, and parasites (e.g., Hanski et al. 2001; Berryman 2002). The other dichotomy is between the single-factor school, which considers a single factor (intrinsic or extrinsic) as the primary cause of population cycles, with other factors playing only secondary roles (Hanski et al. 2001), and the multifactor school, which argues that no single factor is sufficient to explain rodent population cycles, and that multiple factors (intrinsic or extrinsic) must interact to cause population cycles (e.g., Lidicker 1988). There is no one-to-one correspondence of hypotheses with particular theories or models. Some hypotheses were clearly motivated by theoretical models or schools of thought (e.g., the predation hypothesis postulates a single extrinsic factor); others were based on biological intuition (e.g., most intrinsic hypotheses), although some were subsequently modeled to test their potential to generate cyclic dynamics in rodent abundance.

Predator–prey dynamics and the specialist predator hypothesis.—Models of predator–prey dynamics are the most intensively studied mechanistic models of population cycles (Hanski et al. 2001; Turchin 2003), and typically are formulated as two-dimensional systems of differential equations. Various versions of predator–prey models differ mostly in how the functional response is modeled and whether or not the effects of generalist predators are included (reviewed in Hanski et al. 2001; Turchin 2003). One version of the predator–prey model (Hanski et al. 1991) generates prey population dynamics that are strikingly similar to cyclic dynamics exhibited by voles in Fennoscandia.

The predator hypothesis asserts that predation by specialist predators generates second-order dynamics via a time lag in their own reproductive response to increasing prey populations. Complementing this, however, generalist predators can switch prey readily in response to variation in prey numbers, thereby depressing multiple prey populations without a time lag, and imposing direct DD. Specialist predators should generate delayed DD, resulting in cyclic dynamics, whereas generalist predators may determine the length and amplitude of the cycle. Consequently, both specialist and generalist predators may be necessary and sufficient to cause rodent population cycles, as well as the latitudinal gradient in cyclicity observed in Fennoscandia (e.g., Hanski et al. 2001; Korpimäki et al. 2002). In combination, specialist and generalist predators create a pattern of autocorrelation in prey population dynamics that may be characteristic of 3- to 5-year rodent cycles (Hanski et al. 2001; Turchin 2003).

The predation hypothesis has been tested using observational and modeling studies, as well as field experiments (reviewed in Hanski et al. 1991, 2001; Krebs 2013). Experimental studies suggest at least three general observations. First, nomadic avian predators track vole abundance (without a time lag) but do not

substantially depress vole abundance, leading to the conclusion that they could not cause rodent cycles (although they might cause geographic synchrony in population cycles—Norrdahl and Korpimäki 1995; Korpimäki and Norrdahl 1998; Korpimäki et al. 2002). Second, experimental reduction in densities of all main predators prevents vole population declines, whereas populations continue to decline in control areas (Korpimäki and Norrdahl 1998). Finally, reduction in abundance of all main predators during summer and fall increased the fall vole density 4-fold during the low phase and 2-fold during the peak phase, and delayed the initiation of the decline phase (Korpimäki et al. 2002). These results suggest that, at least in northern Europe, specialist predators drive summer declines of rodent populations (Korpimäki and Norrdahl 1998), and cause population cycles similar to those observed in cyclic rodent populations (Korpimäki et al. 2002).

Outside of Fennoscandia, however, empirical evidence for the role of specialist predators (or predators generally) is mixed. Summer density and survival of brown lemmings (*Lemmus trimucronatus*), as well as nest density during the winter, were higher where aerial and terrestrial predators were excluded by fencing, relative to that in a control grid, suggesting that predators may limit brown lemming populations (Fauteux et al. 2016). Similarly, collared lemmings (*Dicrostonyx groenlandicus*) protected from predators via fencing experienced higher survival but did not grow faster than did an unprotected population (Reid et al. 1995). Unfortunately, both of the preceding studies suffer from a lack of replication (e.g., a single exclusion plot). The strongest evidence contradicting the specialist predator hypothesis comes from long-term research at the Kielder Forest, United Kingdom, where experimental reduction of least weasel (*Mustela nivalis*) abundance (by livetrapping and removal) failed to stop population cycles of field voles (*Microtus agrestis*—Graham and Lambin 2002).

Vegetation–rodent models and food hypotheses.—Bottom-up processes might regulate rodent numbers directly (e.g., via changes in quantity or quality of food) or indirectly (e.g., via soil nutrients). Periodic overexploitation of food resources causes populations to crash due to starvation; the time required for vegetation to regrow or for soil nutrients to be replenished could introduce a delayed effect needed to cause population cycles. Consequently, rodent–vegetation interactions have long been considered as an important factor causing, or at least contributing to, population cycles (Pitelka 1957, 1964).

Studies that have tested the food hypothesis using experimental exclosures have reported mixed results regarding the effect of herbivores exclusion on biomass of vascular plants. Johnson et al. (2011) reported that the biomass of different plant functional groups (but not species diversity) differed in long-term herbivore (mostly brown lemming) exclosures near Barrow, Alaska, relative to control plots, although this appeared subordinate to the influence of habitat type. In particular, exclusion of brown lemmings in dry tundra led to a lichen-dominated plant community, whereas that in wet tundra was dominated by mosses (Johnson et al. 2011). In a related report, Villarreal et al. (2012) noted that the greatest changes in the cover of

different plant functional groups at these sites coincided with a brown lemming population irruption. In Sweden, rodent exclusion led to increased plant biomass over 14 years of monitoring (Olofsson et al. 2012). However, no evidence suggests that rodent population crashes are due to overgrazing or food shortages alone.

A direct approach to test the food hypothesis is to provide supplemental food to experimental populations, with the expectation that supplementation should stop population cycles (Krebs 2013). Although food supply affects many aspects of rodent ecology, it has not been shown to prevent or substantially alter population cycles (for reviews, see Boutin 1990; Prevedello et al. 2013), suggesting that changes in food supply are neither necessary nor sufficient to cause population cycles (Krebs 2013). Indirect tests of the food hypothesis via fertilization experiments at Barrow, Alaska, failed to elicit a positive demographic response by brown lemmings (Pitelka and Batzli 2007). Although consumer–resource dynamics can generate population cycles, rodent–vegetation models (represented as two- or three-dimensional differential equations) analyzed under a variety of scenarios failed to generate cyclic dynamics with 3–5 year periodicities (Turchin and Batzli 2001).

Host–parasite dynamics and the disease hypothesis.—Parasites may delay maturation and reproductive rates in small mammals that cycle in a density-dependent manner (Telfer et al. 2005). Smith et al. (2008) modified the classic SIR (susceptible, infected, recovered) model of host–pathogen dynamics (Anderson and May 1992) to test if rodent–pathogen interactions could generate population cycles. They concluded that diseases with brief infection periods, combined with slow recovery of reproductive function once hosts recover from the disease, could generate high amplitude, multiannual population fluctuations, and that vole–parasite interactions may explain population cycles in northern England (Smith et al. 2008, 2009). In contrast, Deter et al. (2008) modeled the demographic consequences of infection by a trematode parasite (*Trichuris arvicolae*) of three species of voles, suggesting that this parasite could regulate at least one of these species, but that it does not generate cyclic fluctuations in abundance. However, no compelling evidence suggests that pathogens or parasites are necessary or sufficient for population cycles to occur.

Maternal effects model and hypothesis.—Inchausti and Ginzburg (1998, 2009) postulated that nongenetic transmission of quality from mother to offspring causes population cycles. They assumed that maternal “quality” (vaguely defined) changes in a density-dependent fashion, which in turn influences population dynamics. They formulated this as a two-dimensional system of difference equations which model the coupled dynamics of rodent population and maternal quality in spring and fall, respectively. However, the periodicity of cycles generated by this model is generally inconsistent with those observed in nature, and unrealistically high survival rates (> 0.95 per month) are needed to generate cycles with more realistic periodicity (e.g., of 3–5 years—Turchin 2003).

Other intrinsic hypotheses.—Four other intrinsic mechanisms have been proposed to explain rodent population cycles (Krebs 1996, 2013). The *polymorphic behavior-genetic* (or *Chitty*) *hypothesis* invokes genetic changes, consequences of frequency-dependent or DD natural selection on life-history traits, as the cause of population cycles. The *stress hypothesis* was motivated by the idea that chronic nonspecific stressors (e.g., high population density, aggression, predation risk) trigger physiological responses that affect behavioral, physiological, and life-history traits over multiple generations (Christian and Davis 1964). The *sociobiological hypothesis* invokes spacing behavior to explain phase-related changes in demographic parameters (Charnov and Finerty 1980). The *environmentally mediated individual quality hypothesis* proposes that phase-related changes in individual quality (without specifying the meaning of quality) cause phase-specific patterns of demographic characteristics and thus population cycles (Ergon et al. 2001; Oksanen et al. 2012). However, no conclusive evidence shows that intrinsic factors alone are either sufficient or necessary to cause population cycles. Indeed, the Chitty hypothesis has been experimentally rejected (Boonstra and Boag 1987), and evidence for the other intrinsic hypotheses is mixed or inconclusive (Ergon et al. 2001; Norrdahl and Korpimäki 2002; Oksanen et al. 2012).

The only single-factor hypothesis that has received substantial experimental support is the (specialist) predator hypothesis. However, the experimental rejection of this idea in northern England, and the lack of evidence for a delayed numerical response of specialist predators in the United Kingdom, France, and eastern Europe (Lambin et al. 2006), raises questions regarding the universality of the hypothesis.

Models invoking multiple factors, and multifactorial hypotheses.—Lidicker (1978, 1988, 2000) proposed that multiple factors (at least four intrinsic and four extrinsic) underlie cyclic population dynamics in California voles (*M. californicus*), and that the relative roles of these factors vary across density phases and over time and space. This multifactorial perspective can explain annual or multiannual population fluctuations, spatiotemporal variations, and biological attributes of cycles, and is conceptually appealing in light of the failure of simpler, one- to two-factor hypotheses, to explain population cycles. Most field experiments of the multifactorial hypothesis manipulated the two obvious potential drivers of rodent cycles—food and predators. Results have consistently shown that the population-level effect of food supplementation and predator exclusion (or removal) was greater than that of either treatment alone (Klemola et al. 2000; Prevedello et al. 2013). Although primary productivity or food supply may modulate the impact of predators on prey populations (e.g., Oksanen and Oksanen 2000), no experiments have succeeded in stopping or substantially altering cyclic population dynamics. Few studies have experimentally tested for effects of three or more factors on cyclic rodent populations (but see Taitt and Krebs 1983; Krebs et al. 1995; Batzli et al. 2007).

Klemola et al. (2003) used stage-structured matrix population models to test for the potential influence of vegetation and predators on the population dynamics of voles and lemmings.

Their simulations indicated that trophic interactions could produce cyclic changes in abundance, although modeled dynamics did not adequately capture the shape or amplitude of cycles observed in natural rodent populations. They suggested that assumptions about phase-dependence in trophic interactions, or some population-intrinsic factors, may be required to generate realistic population cycles and, consistent with [Lidicker \(1978, 1988\)](#), that trophic interactions may be necessary but not sufficient to cause population cycles that are similar to those observed in nature. In the only individual-based modeling approach that simultaneously considers both intrinsic and extrinsic factors, [Radchuk et al. \(2016\)](#) showed that one extrinsic (predation) and two intrinsic (sociality and dispersal) factors could generate population cycles that are comparable to those observed in the field. Again consistent with a multifactorial approach, only their full model, including all three factors, yielded population cycles with periodicity, amplitude, and fall densities that were comparable to those observed in northern Fennoscandia.

In conclusion, nearly a century of research has yielded many biological insights, but the underlying causes of population cycles are yet to be ascertained. While the predation hypothesis has received experimental support in Fennoscandia, predation alone cannot explain population cycles everywhere. Finally, some field experiments and modeling studies suggest that a combination of intrinsic and extrinsic factors underlie rodent population cycles. Clever field experiments that manipulate both intrinsic and extrinsic factors are needed to solve the enigma of population cycles ([Krebs 2013](#)).

SPECIES INTERACTIONS

Interspecific Competition

Interspecific competition influences virtually all facets of population and community ecology, in turn structuring patterns of biodiversity at higher spatial scales. Numerous foundational principles in ecology reflect the pervasive nature of competition, including limiting similarity and competitive exclusion, competitive release, character displacement, the structure and nature of the niche, and optimal foraging theory. The outcome of competition may be context-dependent. For example, Norway rats (*Rattus norvegicus*) replaced black rats (*R. rattus*) in Britain, whereas the latter replaced the former in the forests of New Zealand ([King et al. 2011](#)). [King et al. \(2011\)](#) argued that the smaller size and greater climbing agility of *R. rattus* likely give it an advantage in New Zealand forests, whereas the larger size of Norway rats provides a competitive advantage in less vertically complex environments such as in the British Isles.

Competition may be inferred from demographic data.—As with intraspecific competition, analyses of time-series data can uncover interspecific competition. [Marshall et al. \(2016\)](#) applied almost 2 decades of aerial surveys to conclude that competition, in particular with common waterbuck (*Kobus ellipsiprymnus*), was the strongest factor depressing southern sable antelope (*Hippotragus niger*) numbers in South Africa.

Life-table analyses implicate competition with African lions as a dominant influence on the demography of spotted hyenas (*Crocuta crocuta*—[Watts and Holekamp 2009](#)).

Short-term data may also confirm competition. Under experimental conditions, the presence of field voles delayed breeding by weanling bank voles (*Myodes glareolus*), but had no effect on weanling survival ([Eccard et al. 2002](#)). In contrast, adult female bank voles experienced lower survival and reduced territory size due to direct interference competition (rather than indirect exploitation) with field voles, but this did not affect body weight or litter sizes ([Eccard and Ylonen 2002](#)).

Experimental manipulation may unmask competition.—[Stewart et al. \(2005, 2011\)](#) manipulated the density of elk to show that elk and sympatric mule deer had greater dietary diversity and diet overlap where elk abundance was higher, and that elk body condition and pregnancy rates were lower at high density. Exclusion of Australian swamp rats (*R. lutreola*) from replicate study sites in New South Wales led to a 6.5-fold increase in capture rate of Australian bush rats (*R. fuscipes*), a putative competitor ([Maitz and Dickman 2001](#)).

Competition may lead to character displacement and niche differentiation.—Where niche overlap is substantial, species may diverge morphologically (character displacement) or adjust their realized niche (niche differentiation). Character displacement has an extensive legacy in the ecological literature ([Pfennig and Pfennig 2012](#)) and remains controversial ([Hulme 2008](#)). In North America ([Gannon and Racz 2006](#)) and Europe ([Postawa et al. 2012](#)), morphologically similar bat species (*Myotis* spp. and *Plecotus* spp.) exhibited character displacement in sympatry, with one species of each pair shifting cranio-trophic morphology to forage on different prey items, presumably to reduce or avoid competition. In Finland, female European red foxes (*Vulpes vulpes*) displayed increased cranio-dental adaptations for a carnivorous diet following the invasion of a putative competitor, the raccoon dog (*Nyctereutes procyonoides*—[Viranta and Kauhala 2011](#)).

Niche differentiation also reflects interspecific competition. Snow leopards (*P. uncia*) are similar in size to common leopards and both prey on similar species in the central Himalaya. Trophic overlap may be mitigated by habitat segregation between these species (high elevation grass- and shrubland versus lower elevation forest, respectively—[Lovari et al. 2013](#)). At the other end of the body size spectrum, similar sized shrews (*Neomys fodiens* and *N. anomalus*) in Germany segregate by microhabitat ([Keckel et al. 2014](#)).

The growing use of stable isotopes is shedding light on patterns of trophic differentiation among ecologically similar species. Confirming theoretical expectations, stable isotopes have shown that syntopic species of rodents ([Codron et al. 2015](#)) and bats ([Dammhahn et al. 2015](#)) occupy distinct isotopic niches, and species with strongly overlapping isotopic niches generally do not co-occur.

The ease with which food resources may be readily manipulated for some species has facilitated use of experimental approaches to characterize the presence and strength of

competition. Studies using GUDs have confirmed both interference and exploitative competition in Israeli gerbils (*Gerbillus* spp.—Ziv and Kotler 2003), and shown that these can reduce intrasexual competition in the subordinate species (Ovadia et al. 2005; see “Intraspecific Competition” section). The experimental use of GUDs helped explain why red-backed voles (*M. gapperi*) decline following forest harvesting in Quebec; although competition and predation risk increased with disturbance in a harvested patch, competition (both inter- and intraspecific) was the primary mechanism leading to population declines (Lemaître et al. 2010).

Another approach has been to measure spatial or temporal variation in activity (e.g., “activity density”). Abramsky et al. (2000) quantified activity using sand-tracking plates in experimental arenas, and showed that Allenby’s gerbil responds gradually and consistently to artificially changing competitor regimes (both intra- and interspecific). They also quantified the energetic cost of interference competition, showing that an additional 1.8–3 g of seeds ($\text{day}^{-1} \text{ ha}^{-1} \text{ individual}^{-1}$ —Abramsky et al. 2001) was sufficient for Allenby’s gerbil to become active in the face of competition with the larger greater Egyptian gerbil (*G. pyramidum*).

Negative spatial or temporal associations may suggest competition even though they are correlational. Strong negative spatial correlation between the abundances of sympatric antelope wallaroos (*Macropus antilopinus*) and eastern gray kangaroos (*M. giganteus*) suggests interspecific competition (Ritchie et al. 2008). Mule deer and white-tailed deer in Oregon exhibit considerable dietary overlap (89–96% seasonally—Whitney et al. 2011), but coexist by spatial segregation, with mule deer favoring higher elevations and greater topographic variation, while white-tailed deer favor lower elevations with lower slopes that are closer to streams. European pine marten and stone marten (*M. foina*) partition habitats almost completely in Poland; the former favor forest and avoid developed areas, while the latter prefer developed regions (Wereszczuk and Zalewski 2015).

Temporal segregation is shown by bats visiting limited water sources in arid regions of Colorado (Adams and Thibault 2006), and by red brocket deer (*Mazama americana*, mostly nocturnal) and similar-sized and sympatric gray brocket deer (*M. gouazoubira*, mostly diurnal) in Brazil (Ferreguetti et al. 2015). Of course, many species employ a combination of spatial and temporal partitioning. Free-roaming domestic cats (*Felis catus*) partition the landscape with coyotes (Gehrt et al. 2013), but where spatial segregation is not possible, they segregate temporally (Kays et al. 2015).

The ghost of competition past.—This term has two relatively distinct meanings in the literature. The concept was introduced by M. L. Rosenzweig in a 1976 seminar at the University of California Santa Barbara (M. L. Rosenzweig, University of Arizona, pers. comm.), to refer to competitive dynamics between species in a specific mathematical model of two-species competitive interactions (outlined in Rosenzweig 1989; see also Brown and Rosenzweig 1986; Rosenzweig 1991). In particular, if two regionally sympatric species exhibit distinct habitat

preferences but shared secondary habitat tolerances, there should be an area in density-space (a biplot of the population densities of two species; e.g., an isolog diagram) where each species selects a favored habitat and consequently they do not co-occur (Rosenzweig 1979, 1981). While the lack of syntopy is rooted in competitive interactions between these species, competition would not be detected by traditional field studies; hence, a ghost of past competitive interactions. The concept was subsequently expanded by Connell (1980) to refer to any form of past competition, and he dismissed it as an explanation for the absence of evident competition in extant communities.

Proving past competition is challenging, and often impossible, but by returning to the original definition and applying isodar methods, Morris (1999; Morris et al. 2000) has done so successfully. For example, lemmings (*D. groenlandicus* and *L. trimucronatus*) and tundra voles (*M. oeconomus*) compete asymmetrically for habitat at high densities, but at usual population densities they have distinct habitat preferences, so that competition is trivial, consistent with predictions based on the ghost of competition past (Morris et al. 2000; Ale et al. 2011).

Competition may alternate with facilitation.—Animals may compete under one set of conditions and not under others. African lions compete strongly with spotted hyenas in Kenya (Watts and Holekamp 2009), but they appear to coexist in Zimbabwe by increasing opportunities for scavenging (e.g., intraguild facilitation—Periquet et al. 2015). The competition–facilitation continuum has been studied more extensively in grazing mammals. Prairie dogs (*Cynomys* spp.) compete with ungulates for food resources under some conditions, yet facilitate these same ungulates under other conditions (Augustine and Springer 2013; Sierra-Corona et al. 2015). Arsenault and Owen-Smith (2002) argue that facilitation likely is an ephemeral association, restricted to growing seasons when food is abundant (although it is critical to distinguish actual facilitation from positive correlations caused by shared responses to limiting factors or shared habitat preferences—D. W. Morris, Lakehead University, pers. comm.). However, they also note that seasonal facilitation could exceed exploitative competition that follows during less productive seasons, as confirmed for herbivores in South Africa (Arsenault and Owen-Smith 2011) and ungulates in North America (Hobbs et al. 1996), Kenya (Young et al. 2005; Odadi et al. 2011), and India (Dave and Jhala 2011). du Toit and Olff (2014) argued for the primacy of competition over facilitation in structuring large herbivore assemblages when resources are limiting, but facilitation through shared predators (e.g., apparent competition) may be more common than generally understood (Sundararaj et al. 2012).

Further work should continue to evaluate the *relative* role of competition in structuring populations and communities and to clarify when and where competition assumes priority over other types of interactions. This is particularly important in the face of global anthropogenic effects on habitats, most notably desertification and climate change, and provides a vehicle for integration of fundamental ecological investigation into increasingly critical conservation research.

Predation

Predation is a driving force in the ecology and evolution of mammals. Scientific understanding of predation is deeply rooted in the coupled consumer–resource Lotka–Volterra model developed nearly a century ago (Lotka 1925; Volterra 1926), and studies of large and small mammals continue to play a central role in predation research. Predation may operate directly through the mortality of prey, or indirectly through fear or via linkages with intermediate species. Here we emphasize indirect effects of predation, which have received much attention recently.

Shared predation has implications for ecology and conservation.—Current theoretical understanding of predation has developed in large part by adding layers of complexity to basic consumer–resource models, and testing these models in the field. This is well-exemplified with the concept of asymmetrical apparent competition, in which a primary prey species has a negative indirect effect on a secondary prey species by supporting a shared predator (Holt 1977; Holt and Bonsall 2017). Apparent competition and hyperpredation are key interactions in conservation problems worldwide (DeCesare et al. 2010; Holt and Bonsall 2017; see “Foraging Ecology” section). For example, feral domestic pigs (*S. scrofa*) in the California Channel Islands enabled colonization by mainland golden eagles (*Aquila chrysaetos*), and incidental predation by the latter drove the endangered island fox (*Urocyon littoralis*) to extinction on some islands (Roemer et al. 2002). Eradication of feral domestic pigs, however, combined with capture and removal of golden eagles, led to the recovery of surviving populations of the island fox (Coonan et al. 2010; Jones et al. 2016). Similarly, altered forest structure in British Columbia allowed moose (*Alces alces*) density to increase, which led to increased density of gray wolves (Serrouya et al. 2011). Increased incidental predation by gray wolves is driving endangered woodland caribou to extinction. A large-scale experimental reduction in moose density resulted in reduced gray wolf density, secondarily stabilizing woodland caribou populations (Serrouya et al. 2015a, 2015b). These examples demonstrate the ability of models of apparent competition and predator–prey dynamics to predict conservation outcomes (Holt and Bonsall 2017).

Intraguild predation is another triangular species interaction involving shared predation. In this case, an apex predator preys on an intermediate “mesopredator” and shared prey (Polis et al. 1989). Triangular interaction motifs such as intraguild predation and apparent competition are common in food webs and can strongly influence community structure and stability (Polis and Strong 1996; Vance-Chalcraft et al. 2007). When apex predators and mesopredators share prey, intraguild predation theory predicts that extirpation of the apex predator could negatively affect prey because the mesopredator should be a more efficient consumer (Polis et al. 1989; Robinson et al. 2014). Indeed, numerous cases of “mesopredator release” have been documented, with the loss of an apex predator indirectly depressing prey populations via mesopredator release (Prugh et al. 2009; Ritchie and Johnson 2009).

Understanding such intraguild interactions has enhanced predictions of the likelihood of undesirable side effects of predator management. For example, removing invasive domestic cats from islands to protect nesting birds can increase nest predation if invasive black rats also occur on the islands, since black rat predation on bird eggs can exacerbate declines in bird populations (Fan et al. 2005; Rayner et al. 2007). Similarly, gray wolf control in Alaska, which is conducted to increase ungulate abundance, could reduce the population growth of Dall’s sheep (*O. dalli dalli*) if coyote populations are released from suppression by gray wolves, because coyotes kill more Dall’s sheep than do gray wolves (Prugh and Arthur 2015).

Although continental-scale correlative studies generally report negative associations between large and small carnivores (Elmhagen and Rushton 2007; Johnson et al. 2007; Newsome and Ripple 2015), research at local scales often fails to support the predicted suppressive effects (Gehrt and Prange 2007; Schuette et al. 2013; Steinmetz et al. 2013). Continental-scale analyses that compared indices of mesopredator abundance at the core versus edge of large carnivore distributions indicate that large carnivore density may need to exceed a threshold for mesopredator suppression to occur, and that large carnivores may not have strong top-down effects at range edges (Newsome and Ripple 2015; Newsome et al. 2017). In addition, scavenging (Fig. 1) may be a key interaction involving carnivores that leads to contrasting scale-dependent patterns. For example, Sivy et al. (2017) examined interactions among gray wolves and a suite of five mesocarnivore species in areas with and without gray wolf control, and found that positive local-scale associations between gray wolves and scavenging mesopredators led to suppression of mesopredators by gray wolves at the landscape scale. Opportunistic mesopredators commonly scavenge kills of larger carnivores, and this subsidy can be an important food source in areas where they coexist (Wilmers et al. 2003; Elbroch and Wittmer 2012; Sivy et al. 2018). However, scavenging also increases the risk of intraguild predation (Merkle et al. 2009), presenting a potentially intense risk-reward trade-off. Scavenging and intraguild predation may be inextricably linked for carnivores, and the joint study of these distinct yet related interactions across spatial scales is an exciting new frontier in predation research (Moleon et al. 2014; Pereira et al. 2014).

Nonlethal effects of predation may exceed lethal effects.—Extension of classic two-species Lotka–Volterra models to three-species models of apparent competition and intraguild predation has substantially improved our understanding of predator–prey dynamics. However, these models assume that the effects of predation are purely consumptive, thereby ignoring nonconsumptive “fear” effects. Pioneering experiments examining foraging behavior of desert rodents based on GUDs revealed that foraging costs associated with predator avoidance can be substantial (Brown et al. 1994, 1999; Brown and Kotler 2007; Prugh and Golden 2014). Nonlethal effects of predation include reduced foraging efficiency and increased physiological stress (Creel 2011; Clinchy et al. 2013), and the strength of these effects on prey population growth may exceed those of the



Fig. 1.—Apex predators, such as these gray wolves from Denali National Park (Alaska), may have indirect effects on smaller mesopredators species through direct mortality (intraguild predation) and via indirect pathways such as providing carcasses for scavenging. These effects may vary from local to landscape scales. Photo by L. R. Prugh.

direct lethal effects of predation (Preisser et al. 2005; Wirsing et al. 2008). For example, rates of egg predation by an endemic deer mouse (*P. m. elusus*) on Santa Barbara Island (California) were unrelated to deer mouse density, and instead depended on the risk of owl predation that was perceived by deer mice when foraging (Thomsen and Green 2016). The relative importance of lethal versus risk effects of predation for ungulate populations has been the subject of numerous recent studies (Moll et al. 2017) and ongoing debate, with a strong focus on gray wolves and elk in Yellowstone (Creel et al. 2013; Middleton et al. 2013). Prey naiveté can be particularly consequential on islands, and the effect of invasive predators in many regions has dramatically affected prey populations (see “Invasive Species” section). Studying the strength and context-dependency of risk effects is likely to be an active area of future research in which mammalian species will play a critical role.

Top-down or bottom-up?—The relative importance of top-down and bottom-up effects on community dynamics is an enduring debate that is increasingly relevant to conservation because global change affects both bottom-up resources and the abundance of top predators. The exploitation ecosystem hypothesis (EEH) predicts stronger top-down effects in more productive systems (Oksanen et al. 1981); specifically, that above a productivity threshold where both herbivores and predators can be supported, herbivore abundance should increase with productivity where top predators are absent or rare (e.g., Arctic systems, or places where predators have been removed). Where productivity is sufficient to support more abundant predator populations, however, plant and predator abundance should co-vary positively and herbivore abundance should remain stable across productivity gradients due to top-down control. Several recent tests of these EEH predictions provide strong empirical support (Elmhagen et al. 2010; Letnic and Ripple 2017; Pasanen-Mortensen et al. 2017), adding clarity to the mechanisms by which bottom-up and top-down factors can interact to influence multitrophic population dynamics.

Although low primary productivity may constrain the potential for top-down control, saturating functional responses and territoriality may also limit the ability of top predators to suppress prey if the latter can respond rapidly and strongly to increases in productivity. This could allow prey to escape top-down control in productive systems (Sinclair and Krebs 2002; Melis et al. 2010). The extent to which large carnivores exert top-down influences in human-modified landscapes is unknown and should be a high priority for future research (Oriol-Cotterill et al. 2015; Kuijper et al. 2016).

Mutualisms

Mutualisms are jointly beneficial interactions between members of different, often phylogenetically disparate, species, and have long fascinated biologists seeking to understand the ostensible paradox of cooperation among organisms (Bronstein 2015). Although every species is involved in at least one mutualistic relationship, ranging from diffuse and facultative to tightly coevolved obligatory species dyads (Herre et al. 1999; Wade 2007), mutualisms have proven difficult to quantify, even for the most charismatic and visible of species.

Facultative mutualisms.—Diffuse and facultative mutualisms involve general adaptations for interactions with many populations or functional groups (Wade 2007). Mammalian examples include facilitation resulting from habitat modification or ecosystem engineering, such as that observed between prairie dogs and large ungulates in North America. The former clip vegetation, which leads to increased nitrogen availability and enhanced foraging opportunities for ungulates (Fahnestock and Detling 2002), while the latter incidentally reciprocate by grazing, thereby reducing visual obstructions for the colonial sciurids (Krueger 1986). Mammals can be involved in “apparent mutualisms,” where a predator becomes satiated by the abundance of a primary prey species and, consequently, an alternative prey species benefits from the presence of the first (Holt 1977); for example, the presence of migratory herds of wildebeests (*Connochaetes taurinus*) and zebras (*Equus quagga*) reduces predation pressure by African lions on their secondary prey (giraffe calves [*Giraffa camelopardalis*]), leading to enhanced recruitment for the latter (Lee et al. 2016). Mutualisms can also take the form of cooperation between species, such as between American badgers (*Taxidea taxus*) and coyotes that jointly hunt ground squirrels, which increases foraging success for both taxa (Minta et al. 1992). Such facultative mutualisms often include multiple phyla. Notably, mammals are important seed dispersers, consuming fruiting bodies and concomitantly scarifying seeds, thereby enhancing germination (e.g., Carvalho et al. 2017; Oleksy et al. 2017) and plant recruitment (Lieberman et al. 1979). The consequences of mammalian mutualisms on plant communities can be wide-ranging—carnivores and larger-bodied mammals, due to large home ranges and strong dispersal power, can be important for long-distance dispersal of plants (Hickey et al. 1999; Jordano et al. 2007). The consequences can also be long-lasting, with fruit traits of some Neotropical plants described as shaped by “ghosts of mutualisms past” from large-bodied mammalian seed dispersers of the

Pleistocene (Janzen and Martin 1982). Mammals are important pollinators; bats and nonvolant mammals (marsupials and primates) visit flowers to consume pollen, nectar, and fruit pulp, and thereby provide plants with pollinating services (Carthew and Goldingay 1997; Kunz et al. 2011). Such mutualisms can also involve humans. In addition to the obvious mutualisms with domesticated mammals, nectarivorous bats throughout Mexico pollinate agave (*Agave* spp.) contributing to reproduction and potentially enhancing genetic variability; agave plants are harvested for the production of distilled beverages, tequila and mezcal (Trejo-Salazar et al. 2016). Honeyguides (*Indicator indicator*) and humans in Africa communicate to locate honeybee nests; when found, the human harvests the honey from the nest and the bird is rewarded with the wax combs left behind (Spottiswoode et al. 2016).

Obligate mutualisms.—In contrast with facultative mutualisms, obligatory mutualisms generally are more stable. Complex host–microbial mutualisms play a fundamental role in energy acquisition, chemical detoxification, and immune function for many mammals (McFall-Ngai et al. 2013). Giant pandas (*Ailuropoda melanoleuca*) depend entirely on symbiotic gastrointestinal microbiota for the metabolism of cellulose in their sole food source, bamboo (Zhu et al. 2011), as is the case in ruminants and many other mammalian herbivores (e.g., Van Soest 1994). Moreover, gut microbes are central in the ability of woodrats (*Neotoma* spp.) to detoxify the chemically well-defended creosote bush on which they subsist (Kohl et al. 2014). Indeed, animal–microbial symbioses not only facilitate the host’s ability to persist in particular environments, but can serve as cornerstones for entire ecosystems (Currie et al. 2003; Dubilier et al. 2008). Mutualisms can also involve direct and indirect consequences for multiple species. For example, three-toed sloths (*Bradypus* spp.) host flightless sloth moths (*Cryptoses* spp.), which depend entirely on three-toed sloths for every step of their life cycle. Although there is no apparent direct benefit of the moth to the three-toed sloth, decaying moths in three-toed sloth fur fertilize algae (*Trichophilus* spp.), which are found only on sloths, and the algae in turn provide benefits in the form of enhanced crypsis to the three-toed sloth host (Pauli et al. 2014). Finally, mammals can have strong mediating effects on tightly linked mutualisms for other taxa. In the African savannah, multiple species of ants protect *Acacia* trees from herbivory and, in return, are rewarded with housing and nectar (Palmer et al. 2008). In the absence of browsing by large mammals, however, trees decreased investments to the ants, which shifted the community composition of ant species and altered the behavior of ants, from protection to antagonism toward the tree, ultimately reducing tree growth and survival (Palmer et al. 2008).

Threats to mutualisms.—Because mutualisms link multiple species to a common fate, they are particularly vulnerable to external threats, such as rapid global change (Kiers et al. 2010). Two classic examples of mutualism breakdown include elevated ocean temperatures and coral bleaching, leading corals to expel their zooxanthellae, with subsequent decline of coral ecosystems (Brown 1997; Hoegh-Guldberg 1999), and dramatic

declines in pollinators, especially honey bees, and their services to plants, caused by a range of drivers (invasive species, disease, and climate change—Potts et al. 2010). We are not aware of examples of mutualism breakdown involving mammals from climate change, but the likelihood of increasingly novel biotic communities and ecosystems (Radeloff et al. 2015) raises the specter of breakdown in mammalian mutualisms, especially those involving tightly linked and highly specialized species (e.g., Muchhala 2002). Other perturbations, though, like bushmeat hunting of mammals in Amazonia (especially on tapirs [*Tapirus* spp.] and ateline primates) can disproportionately reduce seed dispersal for trees with large seeds, leading to dramatic changes in forest composition (Peres et al. 2016). This shift in community composition has ecosystem- to global-scale consequences given that these large-seeded tree species possess denser wood and capture more carbon, and therefore have the potential to dramatically alter carbon storage in Neotropical forests (Peres et al. 2016). In addition, herbivores inhabiting degraded forests possess a depauperate community of gastrointestinal microbiota compared to those living within contiguous and relatively intact forests (Amato et al. 2013). Given the profound impact of microbial community composition on acquisition of energy and nutrients from plant material in the digestive system (Clemente et al. 2012), the loss of key symbionts could compromise the fitness of host herbivores (Cho and Blaser 2012; Nicholson et al. 2012). Moreover, recent losses of biodiversity are correlated with reduced diversity of human commensal bacteria, potentially rendering people more susceptible to a range of health disorders (Hanski et al. 2012). Predicting how global change will affect mutualisms and the species involved is uncertain, but represents an important new frontier in ecology and conservation research.

Invasive Species

Mammals play important roles in conservation science, both as important emblems for public awareness and as focal species for investigation. Conservation is addressed elsewhere in this volume (Bowyer et al. 2019), but invasive species are considered here because the dynamics associated with invasion are intrinsically centered on interactions with other species. Biological invasions arise when species are transported outside their native range by human agency, establish a population, and spread in non-native areas. As they interact with native members of the communities that they invade, the effects of invasive non-native species (INNS) on native species and ecosystem processes may range from mild to catastrophic, in extreme cases reorganizing entire ecosystems. The increasing rate and complexity of animal movements by humans, both intentional and accidental, are amplifying the threats associated with invasive species in many regions.

Predicting the invasiveness of species.—Only a fraction of introductions successfully establish, and only a subset of these spread (Williamson 1996). Moreover, only a fraction of those that do spread have deleterious effects, although these species are naturally the subject of disproportionate scientific and practical interest. Although an early generalization (the “tens rule”)

argued that 10% of species transition between each stage of invasion (e.g., introduction to establishment to spread—[Williamson 1996](#)), recent research with invasive mammals has overturned this view.

Estimates of the number of mammalian species that have been introduced have been refined in recent years, building on [Long's \(2003\)](#) original compilation. [Capellini et al. \(2015\)](#) and [Blackburn et al. \(2017\)](#) identified 232 and 306 mammal species, respectively, as having been introduced to areas outside their native distributions (representing 2.6% and 4.7% of mammal species, respectively). Using the same data, [Clout and Russell \(2008\)](#) estimated that 124 mammal species had established self-sustaining wild populations in at least one location outside their natural range, thereby qualifying as successful invaders. Globally, the proportion of mammalian introductions that led to successful invasion (40–53%) is consistent with inference based on all vertebrates introduced between Europe and North America; specifically, once introduced, vertebrates have a substantially higher potential to become established than suggested by Williamson's tens rule ([Jeschke and Strayer 2005](#)).

In addition to helping to understand determinants of transitions between the stages of invasion, macroecologists have determined species traits associated with transitions from introduction to establishment and spread at large spatial scales. Broadly, mammals adhere to processes deemed influential for other organisms. Not surprisingly, introductions involving more individuals and more releases (hence, higher propagule pressure) are generally more successful. Species introduced to a place with a climate similar to that of their native range are more likely to become established and spread ([Duncan et al. 2001](#)). Certain life-history traits predispose some introduced species to establish and spread in a new environment ([Duncan et al. 2001](#); [Kolar and Lodge 2001](#)). For instance, 23 mammal species that established in Australia had a greater area of climatically suitable habitat available, had successfully established elsewhere, had larger overseas (extra-Australian) ranges, and were introduced more times than were the 18 species that failed to establish ([Forsyth et al. 2004](#)).

Several global analyses of mammalian introductions and invasions highlight traits that are either specific to or most evident in mammals, and show that species transported around the world pass through distinct filters that differentially select successful invaders. For fish, birds, and mammals transported between Europe and North America, association with humans, wide latitudinal range, and large body mass were significant predictors of the first stage of invasion (e.g., being selected for introduction—[Jeschke and Strayer 2006](#)).

Humans strongly bias the taxonomic identity (and life-history traits) of mammal species that are transported around the world and that have the opportunity to become invasive. [Capellini et al. \(2015\)](#) applied phylogenetic comparative methods to show that highly productive mammals with longer reproductive life spans were far more likely to be introduced, and the probabilities of these establishing and spreading were further increased by high reproductive output and number of

introductions. The observation that successful invasive species are hyperproductive is consistent with the suggestion that human preferences for game species or those easy to find, transport, and breed, has strongly influenced the choice of species for introduction ([Capellini et al. 2015](#)). Finally, [Blackburn et al. \(2017\)](#) showed that introduced mammal species have much larger native geographic ranges than those of randomly selected mammals, and that they originate from significantly further north in the Northern Hemisphere and from areas with higher human population densities compared to mammal species with no recorded introductions. Hence, species with human affiliations in northern latitudes of Europe were transported to North America, Australia, New Zealand, and South Africa, and generally at temperate latitudes. In short, humans from northern latitudes moved the species that were available and useful to them, and these were generally larger than species that were not selected for transport ([Blackburn et al. 2017](#)).

Although macroecology has delivered novel insights into the historical patterns of mammalian introduction, these may have limited power for predicting future mammalian invasions. Deliberate mammalian introductions are increasingly hindered by heightened awareness concerning the effect of non-native species, and more stringent regulatory frameworks throughout the world. Contemporary pathways, such as the online pet trade, are now more likely to result in accidental introductions of species, with characteristics that differ from those of species transported during the Colonial Era.

The spatial spread of mammalian invasions.—Ever since [Fisher \(1937\)](#) laid the foundation of spatial population dynamics using partial differential equations to model the spread of organisms, case studies with mammals have been used to predict the velocity of the spread of biological invasions. [Skellam's \(1951\)](#) classical diffusion model predicted a wave-like spread of invasions and a linear relationship between time and the square root of the area invaded. Empirical estimates of the asymptotic speed of expansion were derived for introductions of muskrats (*Ondatra zibethicus*) to central Europe ([Skellam 1951](#)), Himalayan thar (*Hemitragus jemlahicus*) to New Zealand ([Caughley 1970](#)), and sea otters that reinvaded California ([Lubina and Levin 1988](#)). The linear spread hypothesis has been robust to the inclusion of additional biological detail to models that had the appeal of mathematical simplicity, but limited biological insight ([Hastings et al. 2005](#)). However, empirical studies show a greater diversity of expansion patterns than suggested by simple models. Thus, while bank voles seemingly spread at a constant speed in Ireland, invasion waves for eastern gray (*Sciurus carolinensis*) and Pallas's squirrels (*Callosciurus erythraeus*) in Italy and France are accelerating, and those of American mink (*Neovison vison*) in Scotland and greater white-toothed shrews (*Crocidura russula*) in Ireland vary greatly according to habitat quality ([Bertolino and Genovesi 2003](#); [White et al. 2012](#); [McDevitt et al. 2014](#); [Dozières et al. 2015](#); [Fraser et al. 2015](#)).

Confronting even highly simplified diffusion models with real data is challenging and requires parameter estimates for population growth rate and diffusion, as well as functional

forms describing how they vary with density and the environment. Diffusion parameters have often been estimated using maps of range spread with limited accuracy or, more rarely, using independent life table or dispersal data (van den Bosch et al. 1992). Few studies make full use of methodological advances that correct for imperfect detection in species distribution modeling (Kéry et al. 2013; see “Advances in Population Estimation” section). However, it is clear that range spread is observed imperfectly and that the expected spatial patterns in detectability could strongly bias inference (Bled et al. 2011). Consequently, a higher level of rigor is needed in the way models are informed by data, especially when seeking to predict the spread of pathogens harbored by invasive mammals (White et al. 2016).

The impacts of invasive mammals on native species and communities.—Invasive species are a leading cause of animal extinction (Clavero and Garcia-Berthou 2005). Even though mammals account for only a small proportion of successful invaders, some of the world’s most nefarious INNS are mammals. These include several rat species (Norway rat, black rat, Pacific rat [*R. exulans*]), the European red fox, the domestic cat, Javan mongooses (*Herpestes javanicus*), several mustelids, including the stoat (*M. erminea*) and American mink, and domestic pig and goat (*C. aegagrus*). The documented negative effects of invasive mammals on native biodiversity have been direct (mediated by predation, browsing, and competition), and indirect (mediated by trophic cascades, disease-linked apparent competition, and habitat degradation). Effects extend to disruption of patterns of materials flow, such as erosion caused by hoofed mammals and consumptions of plants and seeds (Clout and Russell 2008).

The impact of invasive mammals on island communities.—Invasive non-native species that are generalist mammalian predators, including rats (*Rattus* spp.), domestic cats, stoats, and mongoose, have profoundly affected insular biodiversity worldwide, contributing at least in part to 75% of all recorded terrestrial vertebrate extinctions (McCreless et al. 2016). Several meta-analyses that considered the most damaging invaders provide context for the magnitude of the deleterious effects.

1) Rats have reached about 90% of the world’s islands, where they suppress some forest plants and are associated with extinctions or declines of flightless invertebrates, ground-dwelling reptiles, land birds, and burrowing seabirds, with detrimental effects on at least 173 taxa of plants and animals (including 134 vertebrates—Towns et al. 2006). Small burrowing seabirds are most severely depressed (Jones et al. 2008), but even the relatively small Pacific rat and house mouse (*Mus musculus*) can cause significant mortality of albatrosses and petrels that are more than 50 times their size (Wanless et al. 2012). Comparisons between invaded and noninvaded islands, and recovery of plants and seabirds following recent rat eradications, further demonstrate the magnitude of rat effects on vertebrates as well as on seeds and seedlings (Towns et al. 2006).

2) Feral domestic cats introduced on islands are responsible for at least 14% of global bird, mammal, and reptile extinctions, and are the principal threat to almost 8% of critically

endangered birds, mammals, and reptiles (Medina et al. 2011). Additionally, stoats have caused numerous local extinctions of birds in New Zealand (O’Donnell 1996), and have stronger detrimental effects on bird populations than do other introduced predators (Lavers et al. 2010).

Aggravating these issues, most islands have been invaded by multiple non-native species. Evidence of greater than additive effects of multiple mammalian invasions caused by pairwise or multispecies indirect trophic interactions includes three phenomena:

1) The probability that a bird species on an oceanic island has been extirpated is positively correlated with the number of exotic predatory mammal species established on those islands after European colonization ($n = 220$ islands—Blackburn et al. 2004).

2) The impacts of invasive mammalian predators increase when either of two non-native alternate prey species (specifically, European rabbits [*Oryctolagus cuniculus*] and either rats or mice) are introduced. This is consistent with the concept of hyperpredation, whereby introduced alternate prey species may subsidize introduced predator populations, thereby magnifying their effect on native prey species that otherwise would be too scarce to fuel the growth, or sustain a population, of invasive predators (Courchamp et al. 2000; Medina et al. 2011). Such forms of interspecific facilitation can be viewed as a special instance of “invasion meltdown” (Simberloff and Von Holle 1999), accelerating the effects of invasive species through synergistic (amplifying) interactions among these species.

3) On Australian islands, extinction probabilities for large mammals (> 2.7 kg) are higher than those for small species, as expected from island biogeographic theory (Marquet and Taper 1998; Cardillo et al. 2005). For small mammals, the presence of black rats is the strongest predictor of extinction, although this is ameliorated by the presence of a larger introduced predator (domestic cats, European red foxes, or dingoes [*C. l. dingo*]—Hanna and Cardillo 2014), consistent with mesopredator (in this case, black rats) suppression (see “Predation” section). Whereas a regional meta-analysis detected evidence of mesopredator suppression and associated mesopredator release where the apex predator was eradicated secondarily (Hanna and Cardillo 2014), this was not supported by a global meta-analysis (McCreless et al. 2016).

A global synthesis of the effect of mammalian INNS (McCreless et al. 2016) on historic extinctions revealed complex interactions between biotic and abiotic factors, including the presence of invasive rats, domestic cats, domestic pigs, mustelids, and mongooses (but not goats, mice, and rabbits), taxonomic class and flight ability of native species, island size, annual precipitation, and the presence of humans. Extrapolation from such statistical models predicts an extinction debt of 45% of 1,998 extant vertebrate populations threatened by invasive species, unless targeted eradication efforts are undertaken. Such numbers likely are indicative of the magnitude of the challenge of, and potential gains from, proactive interventions. Nonetheless, a growing body of empirical evidence supports hope that eradication of mammalian INNS on

islands will deliver conservation gains, such as demographic recovery, recolonization, or reduction in IUCN threat category (Jones et al. 2016).

Because mammals (i.e., domestic cats, rats, mustelids, and mongooses) are among the world's most nefarious island invaders, mammalogists have made distinctive contributions to understanding predation and trophic interactions. Moreover, work in this context has fostered close reciprocal interactions among theoretical, empirical, and conservation management disciplines.

Feral domestic cats and European red foxes decimate meal-sized mammals in Australia.—Australia harbors a largely endemic mammalian fauna that had been exposed to a restricted guild of predators until the arrival of the dingo about 3,500 years ago (Ardalan et al. 2012). Following the arrival of European settlers and numerous introduced non-native species, Australia suffered a faunal collapse that is ongoing (Woinarski et al. 2015). At least 29 endemic Australian land mammal species have become extinct since the arrival of Europeans in 1788, and an additional 56 are threatened, according to IUCN Red List criteria. Many of the latter are now restricted to a few small islands and fenced areas on the mainland, where they are protected from predation by introduced mammals. Compelling evidence suggests that predation by feral domestic cats and European red foxes is the primary cause of declines, possibly interacting with changing fire regimes (Woinarski et al. 2015).

Australian mammals that fall within the preferred prey size for domestic cats and European red foxes (a so-called “critical weight range” of approximately 35 g–5.5 kg) have been far more likely than larger species to have declined or become extinct (Burbidge and McKenzie 1989), in contrast with the global trend of greater declines for larger mammals (Cardillo et al. 2005). The relationship only holds for terrestrial marsupials (not arboreal) and is most significant for species that occupied low-rainfall regions, primarily in southern Australia (Johnson and Isaac 2009).

A new wave of declines is affecting 19 additional marsupial species in the European red fox-free northern tropics of Australia, where small mammal species, including rodents, that occupy open vegetation with moderate rainfall (savannas) are experiencing severe declines (Fisher et al. 2014). Elucidating the cause of this impending catastrophe is an active area of research, but growing evidence implicates predation by feral domestic cats, interacting with fire and grazing that remove cover and increase predation risk (Kutt 2012; Frank et al. 2014). The lengthy time lag between the spread of domestic cats in northern Australia and the full magnitude of effects becoming evident is particularly worrisome; if such a lag was widespread, it would suggest the existence of a large extinction debt (Tilman et al. 1994; Kuussaari et al. 2009) caused by INNS.

Idiosyncratic impacts of invasive species on native mainland prey.—Because they are part of diverse communities, continental species generally lack the naiveté to predation that characterize their insular counterparts. Despite this, INNS mammals are responsible for the decline of several continental species of mammal. These effects are arguably less widespread

and seemingly restricted to a small number of species with idiosyncratic vulnerabilities. The same processes of predation and of synergies between invasive species documented on islands operate, but the greater spatial heterogeneity of continental areas introduces further complexity to ecological interactions between native and invasive mammals.

The United Kingdom is an island, but sufficiently large that prey are not naïve to the risk of predation. The well-documented effect of the American mink on the Eurasian water vole (Fig. 2—*Arvicola amphibius*) in the United Kingdom illustrates how idiosyncratic vulnerabilities of some native species put them at risk from invasive species. The Eurasian water vole is a large (up to 280 g) rodent that inhabits the riparian fringe of waterways. Historically very abundant in Britain, by 1998 this species no longer occurred at 98.7% of previously occupied sites across England, Scotland, and Wales (relative to the 1939 baseline—Moorhouse et al. 2015). American mink, widespread throughout Europe following escape from fur farms, are the main cause for the catastrophic decline of the Eurasian water vole (Moorhouse et al. 2015); they have invaded all but the extreme northwestern corner of the United Kingdom, a region never colonized by the highly convergent but distantly related European mink (*M. lutreola*—Aars et al. 2001; Fraser et al. 2015; Moorhouse et al. 2015). American mink are generalist predators, exploiting a wide range of vertebrate prey in aquatic and riparian environments. The antipredator responses that Eurasian water voles deploy against native mustelid predators (e.g., stoats or European otters [*Lutra lutra*]) include taking refuge in burrows, or diving in water and kicking mud to confuse the predator. Unfortunately, both are ineffective against American mink. Indeed, female American mink are small enough to fit inside Eurasian water vole burrows, and are adept at catching prey while underwater (Macdonald and Harrington 2003). The vulnerability of Eurasian water voles is compounded by the killing and caching behavior of American mink, such that entire water vole subpopulations, typically comprising 10–20 individuals, may be rapidly decimated upon the arrival of an individual American mink; there is no local coexistence (Aars et al. 2001; Telfer et al. 2001). Because American mink have larger home ranges, multiple adjacent local water vole populations are depleted to extinction in close succession. Eurasian water voles typically are organized as metapopulation networks, including a set of local populations experiencing frequent extinction–colonization dynamics. Thus, the overall effect of elevated local population extinction rates under the influence of American mink causes a disequilibrium between extinction and colonization rates, which gradually translates into a metapopulation-wide decline to extinction (Telfer et al. 2001). However, time delays caused by metapopulation dynamics typically are long and may conceal extinction debts (Hanski and Ovaskainen 2002).

The dynamics of species at continental scales play out across gradients of habitat quality for both native and invasive species. This may lead to refuges from predation and allow persistence of vulnerable species in a subset of their pre-invasion range. Such a scenario occurs for Eurasian water voles (Moorhouse



Fig. 2.—American mink (top) are generalist predators and have established invasive populations in southern South America and in Europe. Throughout the United Kingdom they have affected Eurasian water voles (bottom), whose antipredator defenses are ineffective against this invasive predator. Photos by Chris Sutherland (mink) and X. Lambin (vole).

et al. 2015), most obviously in the fringe of Scotland's uplands, where this species has been more resilient to American mink predation than in the lowlands. In the latter habitat, a process similar to spatially explicit hyperpredation unfolds (Courchamp et al. 2000), with a pattern of apparent competition between naturalized European rabbits and Eurasian water voles, mediated by American mink predation (Oliver et al. 2009). In the presence of American mink, Eurasian water voles persist as fugitive species, but only away from valley bottoms colonized by European rabbits; these habitats support American mink that then transiently invade otherwise prey-limited uplands. In the absence of American mink, Eurasian water voles and European rabbits coexist in productive lowlands (Oliver et al. 2009). This highlights the complex and spatially contingent nature of the effect of consecutive species invasions on ecosystems, and underscores how the potential threat of invasive species to native biodiversity may be temporally and spatially complex (Courchamp et al. 2003).

Invasion-mediated hybridization.—Another pernicious effect of invasive species on selected native taxa is mediated by hybridization and genetic introgression. Well-documented examples include the recent hybridization and introgression between native red deer and introduced sika deer (*C. nippon*) that have existed sympatrically in Scotland for about 115 years (Senn and Pemberton 2009). Introgressive hybridization between native species and free-ranging domestic or feral carnivores (e.g., wild domestic dogs [*C. l. familiaris*] and dingo, domestic and wild cats [*F. sylvestris*]) or ungulates (domestic

pigs, goats) can be locally pervasive, threatening the genetic integrity of species and compromising local adaptation (Randi 2008).

Disease-facilitated invasions.—The enemy-release hypothesis (Kolar and Lodge 2001) posits that invasive species may be more successful in their introduced ranges than in their native ranges because of the absence of coevolved natural enemies, including pathogens. An unfortunate correlate of this is that introduced species may transmit novel parasites to hosts in the new range, leading to disease-facilitated invasion (Dunn 2009). An example of this is the displacement of native Eurasian red squirrels (*S. vulgaris*) by invasive eastern gray squirrels in Britain via exploitative competition; this is vastly expedited in the presence of squirrel pox virus, a disease that is lethal to Eurasian red squirrels but asymptomatic in eastern gray squirrels, which act as host and reservoir (Tompkins et al. 2003). In the absence of the pox virus, the effect of eastern gray squirrels on Eurasian red squirrels can be countered with habitat management that is sympathetic to the native species (Gurnell et al. 2006). However, wherever the invasive host reaches sufficiently high density, the non-native pathogen becomes established, and the native squirrel is rapidly replaced (Sainsbury et al. 2008). This introduces both temporal and spatial lags before the full effect of the invasive eastern gray squirrel is evident. An intriguing recent development is that the recovery of the hitherto persecuted native European pine marten reverses the outcome of the competitive interaction between Eurasian red and eastern gray squirrels, as the latter appear naïve to pine marten, and unlike their native counterparts, lack behavioral adaptation to avoid this native predator (Sheehy et al. 2018). At present, unambiguous evidence of a role of pathogens in facilitating mammalian invasion is limited to squirrels, but is increasingly ubiquitous for other taxa (Dunn et al. 2012; Strauss et al. 2012).

Ecosystem meltdown and cascading invasions.—The concept of ecosystem meltdown encompasses the ultimate and most damaging stage of invasion, where INNS profoundly transform ecosystems through a sequence of positive feedbacks resulting from facilitation among INNS (Simberloff and Von Holle 1999). Runaway positive feedbacks in a system create “snowball” effects in which a phenomenon builds on itself in an accelerating fashion, becoming unstoppable. Such processes go beyond accelerating the extinction of native species and lead to profound changes in species assemblages.

One startling example of ecosystem restructuring involves a synergistic trio of invasive mammals, the American beaver (*Castor canadensis*), muskrat, and American mink at the southern end of the Americas (Crego et al. 2016). The ecosystem engineering activities of American beavers convert free-flowing streams into active and abandoned American beaver ponds and meadows that do not support native *Nothofagus* trees. Muskrats, the dominant prey of American mink in its native range, preferentially occupy American beaver ponds, and they represent > 50% of the biomass of American mink diet in inland environments of southern South America. American mink also consume non-native trout (*Salvelinus fontinalis* and *Oncorhynchus mykiss*) and several native terrestrial species, including

Magellanic woodpecker (*Campephilus magellanicus*), waterfowl, songbirds, and rodents (*Abrothrix olivacea* [prev. *A. xanthorhinus*] and *Oligoryzomys longicaudatus*). Thus, American beavers facilitate the existence of muskrats, which in turn sustain inland American mink populations that have major effects on the native biota, especially birds and small rodents. Because American beavers act as ecosystem engineers, changing forests into wetlands with abundant grasses and rush vegetation (Anderson et al. 2009; Crego et al. 2016), it is doubtful whether the kind of restoration and ecosystem recovery achieved after the removal of long-established Pacific rats on oceanic islands will materialize in the subantarctic environment of extreme southern South America.

CONCLUSIONS AND PROSPECTUS

Scientific understanding of mammalian population ecology and interactions among species has increased substantially in recent decades. Longer-term and broader spatial scale data sets have become available, and movement toward multispecies perspectives, integration of top-down and bottom-up approaches, and development of sophisticated analytical approaches have facilitated insight into broader ecological patterns, frequently establishing mammalian systems as models for basic and applied ecology.

An ongoing challenge for mammalogists is to explain the considerable variation that exists among individuals. This may be particularly relevant to foraging ecology and habitat selection, as these are driven by behaviors that are intrinsically individualistic. Recent conceptual developments in the context of behavioral syndromes and maternal effects may be profitable avenues for consideration.

Rigorous science calls for accurate estimation of populations and distributions. Analytical tools in these areas have improved and diversified greatly over the past 20 years, suggesting that the “state of the art” is an ever-increasing trajectory. The information provided by these models can be used to parameterize predictive population models (e.g., Nichols et al. 1992; Fujiwara and Caswell 2002) and provide insights into the management and conservation status of species and populations (Williams et al. 2002). Combined with other novel data types, such as high-resolution remote sensed data (Pettorelli et al. 2014), emerging and improving statistical modeling techniques provide novel insight into mammal population ecology.

Although the theory underlying source–sink dynamics is well established, convincing empirical evidence of such dynamics in nature is scarce (Runge et al. 2006). This discrepancy results at least in part from the challenging task of accurately measuring patch-specific demographic rates (Wiens and Van Horne 2011). In particular, dispersal has been particularly difficult to quantify (Nathan 2001). Current advances in tracking technology (Wall et al. 2014) increasingly facilitate this task. Moreover, the literature on mammalian source–sink dynamics is dominated by studies on rodents, yet the source–sink dichotomy might not always be an adequate concept for describing spatial dynamics of rodent populations (Diffendorfer 1998). Problematically, the

most widely used methods for monitoring rodent populations—livetrapping of individuals and the collection of mark-recapture data—often overestimate mortality rates, because individuals that leave the study area are assumed to be dead. This methodological shortcoming may lead to a misinterpretation of habitat quality and an overestimation of the prevalence of population sinks (Runge et al. 2006). Large mammals, on the other hand, are generally radiocollared and tracked, yet they remain underrepresented in the source–sink literature.

Interactions among individuals—both within and between species—are diverse, complex, and contingent on local and regional issues, ranging from species composition to habitat and climatic influences. In general, intraspecific competition is generally stronger than interspecific interactions (Tong et al. 2012; Jiang et al. 2015), but the relative roles of competition and predation are less clear. The former may be the stronger influence on habitat selection for collared and brown lemmings (e.g., Dupuch et al. 2014) and more strongly depress population size for red-backed voles (Lemaître et al. 2010), whereas the latter appears to be a more proximal factor in habitat selection of gerbils (Abramsky et al. 1998). This does not dismiss the importance of competition for gerbils (e.g., Mitchell et al. 1990; Abramsky et al. 2001) or of predation for lemmings (e.g., Krebs 2011; Fauteux et al. 2016). Indeed, how extrinsic factors may influence the trade-off between these factors, and how they vary across ecological gradients, remain fertile arenas of study. Complicating this, apparent competition may be difficult to distinguish from interference competition (Morris et al. 2000), and the true frequency of the latter in natural systems is poorly understood. Further work on mechanisms of competition, their dependence on extrinsic drivers, how they vary across ecological gradients, and how they interact with other key processes (predation, parasitism, facilitation) remain core to ecological research and will provide opportunities for researchers into the foreseeable future.

It is perhaps ironic that population cycles and associated dynamics are one of the most comprehensively studied areas in mammalian population ecology, yet underlying causative factors remain elusive. We concur with Krebs (2013) that explanations of population cycles must begin with rigorous and quantitative characterization of phase-specific demography. However, a demographically based research agenda that integrates numerical dynamics with phase-related demographic and behavioral changes is likely to be particularly productive, potentially leading (at least partially) to resolution of a problem that has fascinated generations of ecologists. We remain uncertain, however, that any single model for all cycles will ever appear, and biologists focusing on such dynamics are likely to make greater progress by targeting contextual models that provide explanatory power for particular species and regions.

Predation—nature red in tooth and claw—is particularly interesting to the public, and research in this arena often has controversial implications for conservation, highlighting the importance of rigorous study design and appropriate analyses (Allen et al. 2017). The understanding of predation, including both direct and indirect influences on biotas, has

increased by moving toward multispecies perspectives, integrating bottom-up effects and scavenging into models of predation, and studying the effects of risk (both real and perceived). These are all fruitful topics of future research, and studies of large and small mammals will undoubtedly play key roles. Technical innovations such as animal-borne video (Moil et al. 2007; Loyd et al. 2013) and proximity sensors (Marsh et al. 2011; Ripperger et al. 2016) may facilitate new insights into key components of predation such as encounter rates. Likewise, advances in noninvasive genetic techniques are facilitating the identification of causes of predation (Blejwas et al. 2006; Mumma et al. 2014) and determination of diets (Valentini et al. 2009). While challenging in practice, when testing key questions and assessing management actions (e.g., predator control programs and reintroductions), replicated manipulations are essential for gaining fundamental ecological insights (National Research Council 1997; Ford and Goheen 2015).

Mutualisms are more common and widespread than generally appreciated, and they hold a special place in evolutionary ecology. A spectrum of mutualistic interactions exists, ranging from the diffuse to dyadic and tightly coevolved. Depending on the strength of these relationships, certain mutualisms are likely to be sensitive to habitat modification or other environmental change. In particular, the effect of climate change on eroding or even breaking mutualistic relationships by disrupting the phenological or morphological matching between species represents an important line of future research in ecology. Because mutualisms link the fate of multiple species that transcends higher taxonomic boundaries, the preservation of this ecological interaction, while historically overlooked in conservation, should be considered in the face of rapid global change.

Finally, humans have facilitated the movement of species across the globe. Many invasions fail to establish viable populations, but studies of successfully invasive mammals have been particularly influential in advancing the study of biological invasions. Case studies have motivated and challenged components of general ecological theory concerning trophic interactions, but none of the evidence suggests that exotic mammals differ qualitatively from native mammalian predators. Several processes contribute to temporal delays before the full effect of mammalian invasions become realized; as such, they contribute to an extinction debt that may remain unpaid for an uncertain time period.

Overarching all of these issues is global climate change and other anthropogenic stressors that increasingly influence ecology and demography through ongoing habitat fragmentation and modification, and through climatic adjustments that are likely to result in disequilibrium communities (Graham and Grimm 1990; Svenning and Sandel 2013), as well as phenological mismatches between mammalian foragers and their resources (Bartowitz and Orrock 2016) or their abiotic environment (Plard et al. 2014). From an opportunistic perspective, how and under what conditions these changes will influence behavior, demography, and interactions among species will provide excellent opportunities to empirically test ecological

theory. From a strictly utilitarian perspective, the ability to correctly identify the source–sink status of local populations within larger areas (e.g., administrative or management jurisdictions) will be increasingly important for landscape managers. Collecting the information required for conducting such comprehensive assessments will remain labor-intensive and challenging. Given these constraints, the most parsimonious management strategy likely will be to identify and protect the most valuable local populations and habitat patches within a given management region (Hayward and Castley 2018).

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