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Evolutionary theory as a tool for predicting extinction risk

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Timely and proactive wildlife conservation requires strategies for determining which species are most at the greatest threat of extinction. Here, we suggest that evolutionary theory, particularly the concept of specialization, can be a useful tool to inform such assessments and may greatly aid in our ability to predict the vulnerabilities of species to anthropogenic impacts.

Predicting the fate of species in a changing world

Species vary widely in how they are affected by environmental disturbance. Human-induced changes in the environment expose species to novel conditions that did not exist in their evolutionary past, and responses of species can impact their extinction risk [1]. Quantifying extinction risk is an important goal for conservation biologists and wildlife managers who must identify and prioritize species or populations. However, quantifying this risk is challenging, because populations can decline, stabilize, or even increase in the face of environmental change. Authors have discussed the importance of natural history and evolutionary information for assessing extinction risk [2,3]. These methods often require extensive life-history or detailed distributional data, which are optimized for *r*-selected terrestrial species (e.g., insects), but are less operational for larger and more-threatened *k*-selected consumers, especially those that are inherently rare, elusive, and difficult to study.

A framework for integrating evolutionary concepts (i.e., specialization) into risk assessment that can be applied to identify which ecological mechanisms expose various species to extinction risk is warranted. Much of the discussion on specialization has focused on extreme (generalist and specialist) individual species; however, specialization is a continuum, with most species falling between extremes. Thus, we lack a comparative methodological perspective of how the vulnerability of species can be compared along this quantitative axis for evolutionary traits and how these traits might be integrated into assessments of extinction risk.

Specialization as a tool for assessing ecological resistance

An important principle in evolution is that of specialization. As noted by others [4], ecologists have typically defined a specialist as a 'species that occupies a relatively narrow niche or restricted range of habitats, or alternatively a species or population that selects resources out of proportion to availability.' Specialization is a species-level phenomenon and can be measured in different ways (e.g., diet, temperature, morphology, etc.) and is tied to the concept of trade-offs [5]. The 'jack-of-all-trades-master-of-none' principle implies not only that lower levels of specialization (i.e., generalist) enable species to access a wide array of resource niches with relatively equal effectiveness, but also that there are limitations on the ability to efficiently access certain resources. Specialists should be able to access a single resource more effectively, at the expense of accessing a wider range of resources. This suggests that highly specialized species can be disproportionately vulnerable to human-induced environmental change. Conversely, highly generalized species are likely to be less vulnerable to such pressures. Furthermore, the correlation between phenotypic value and fitness of traits might change between environments, in which specialized traits can become maladaptive under altered selective pressures (Box 1). Recent work on sharks has shown that evolutionarily unique species are suffering declines and becoming increasingly extinction prone at faster rates than their more-generalized counterparts [6]. Here, we discuss three examples that demonstrate how viewing specialization as a continuum can inform our understanding of extinction risk (Figure 1).

Taxonomic case studies

Migratory Pacific salmon

Pacific salmon are notable for their remarkable long-distance migrations from freshwater habitats where they hatch (and return to reproduce) to ocean feeding grounds.

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Box 1. The continuum of specialization affects performance in changed habitats

As shown in Figure IA, specific traits of specialist species (designated S1 and S2) perform well under certain conditions or a smaller subset of resources (environment 1 and 2, respectively). A generalist species (G1) theoretically performs the same in both environments, but can also adapt to become increasingly fit when exposed to conditions that are unlikely to have existed in their evolutionary past (e.g., invasive species; G2). Tiger sharks are apex marine predators and the largest predatory fish in tropical waters worldwide, with recent research suggesting that they are functional, behavioral, and dietary generalists in almost all the ecosystems that they inhabit [6]. Tiger sharks have evolved specialized dentition (Figure IB,C) that has afforded them the ability to cut through the hard carapaces of sea turtles, a preferred prey species that shares a convergent distribution across subtropical and tropical marine habitats globally (Figure ID). Despite massive population declines in sea turtle species over the past century, particularly in the Atlantic Ocean, tiger sharks retain one of the most plastic and adaptive diets of all vertebrates, and their populations seem to be stabilizing or starting to increase despite persistent anthropogenic pressures that are causing other species to decline [6]. Thus, the lability of the cognitive and behavioral processes that dictate foraging and diet may offset the costs that might have been incurred from selective regimes favoring specialized teeth. This case study demonstrates the validity in using a multispecies, multifactor comparative framework for assessing and predicting extinction risk.

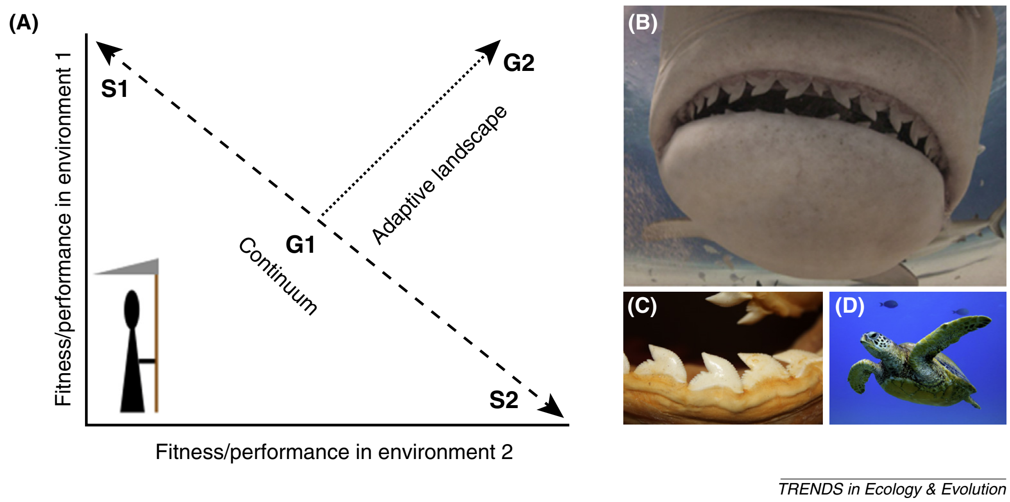

Figure I. The plasticity of ecological traits among threatened vertebrates. Photos B and D used, with permission, from Joe Romeiro and Orvil G. Clark (Oahu, HI, USA), respectively.

Salmon are sensitive to various human-induced environmental changes, including habitat alteration and climate change, and some Pacific salmon populations are critically endangered, while others are extinct [7]. The degree of habitat specialization seems to predict sensitivity to habitat degradation or loss, which can be independent of species range. Species that show extreme philopatry (e.g., sockeye salmon) can be more sensitive to habitat degradation on spawning grounds or rearing areas compared with allopatric species, such as pink salmon. Philopatric tendencies could limit straying when spawning habitats are degraded relative to allopatric species that have flexibility in spawning-ground selection. Physiological specialization is also important, as water and air temperature increase due to climate change. Those salmon populations that can maintain high-performance cardiovascular function at higher temperatures might be more resilient compared with populations that cannot [8]. This reveals the complex nature in which ecological or physiological specialization results in differential resilience to stressors.

Ectothermic lizards

One result of climate change is increases in temperature in different ecosystems, which are expected to increase extinction risk in ectotherms. Recent analyses indicate that global warming could disproportionally impact tropical ectotherms, because these species tend to be thermoconformers, whereas temperate ectotherms in temperate climates tend to be thermoregulators. Theoretical and empirical studies show how the degree of thermal specialization is closely tied both to ongoing population declines in reptiles and future extinction risk [9]. Lizard species that are thermoregulators can better cope with thermal stress compared with thermoconformers, which lack the behavioral capacities to adjust to alterations in temperature. Extreme thermal specialization often occurs in lizards that occupy stable thermal environments, such as montane cloud forests. For example, the Puerto Rican blue-chinned anole (*Anolis gundlachi*) is a thermoconformer that is confined to the cloud forests of El Yunque in Puerto Rico and, thus, faces higher risks from rising temperatures compared with its closely related congener, the crested anole (*Anolis cristatellus*), which is a thermoregulator that can occupy a wide range of thermal environments in and around El Yunque [9,10]. Accordingly, there is strong evidence that montane reptiles and amphibian populations are especially vulnerable to elevated global temperatures, whereas lowland populations are at lower risk [10].

Deep-diving pinnipeds

In marine mammals, successful foraging relies on the interaction between the physiology (i.e., ability to dive), behavior (i.e., how it dives), and the ecology (location and

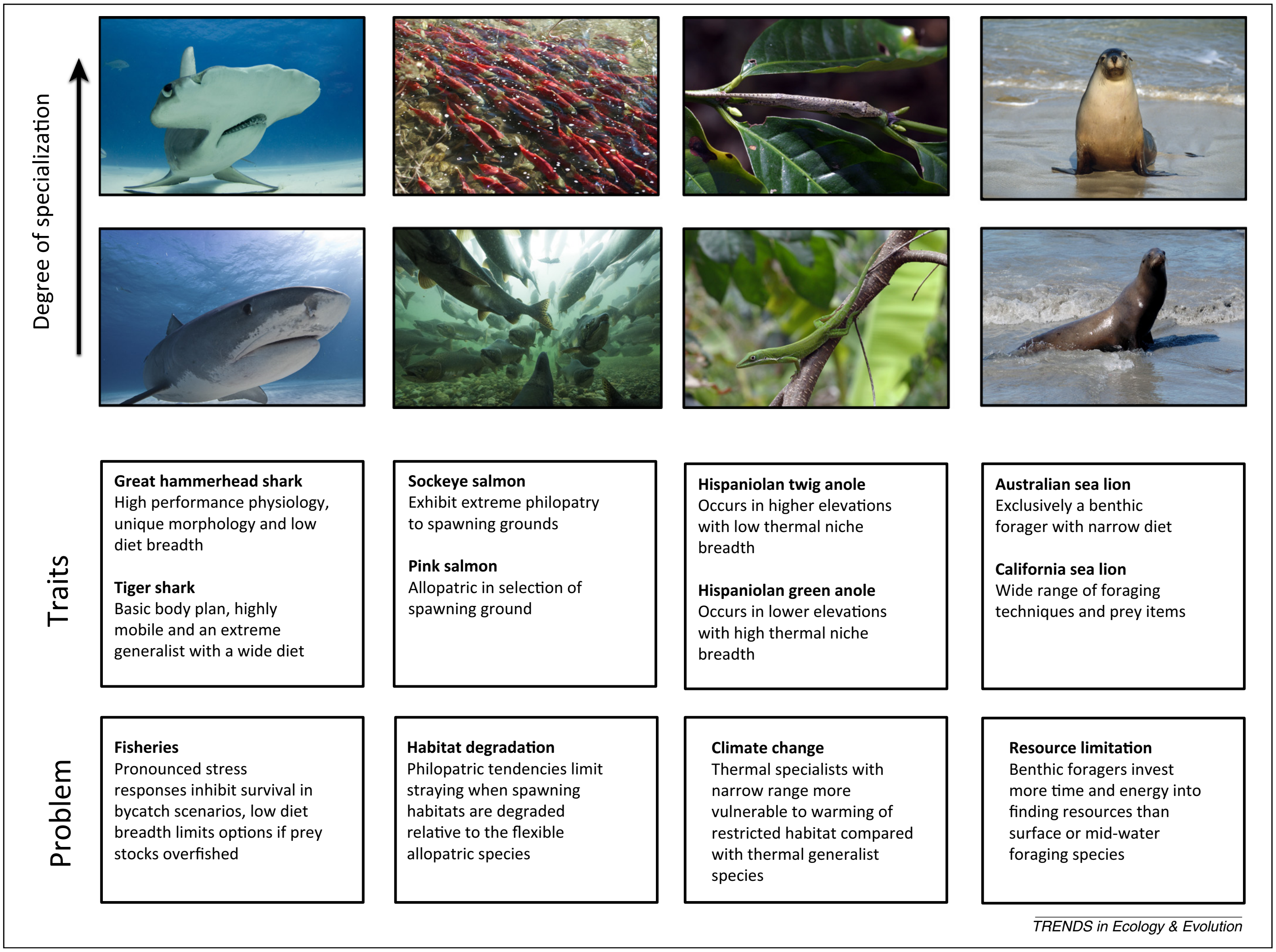

Figure 1. Varying degrees of ecological, functional, and behavioral specialization have differential consequences among vertebrate groups when exposed to human-induced threats: large sharks (great hammerhead and tiger), Pacific salmon (sockeye salmon and pink salmon), anole lizards (Hispaniolan twig anole and Hispaniolan green anole), and pinnipeds (Australian sea lion and California sea lion). Each case study emphasizes the continuum of specialization present in each group by highlighting the outcomes of specialized and generalized species for traits such as physiology and stress responses, behavior and diet, and thermal tolerance. Salmon images reproduced, with permission, from Matt Casselman and Jordan Manley (top to bottom, respectively).

distribution of prey) of the animal. Marine mammals exhibit three foraging patterns: foraging in the epipelagic zone (first 200 m), foraging at or near the ocean floor (benthic or demersal foragers), and foraging in the mesopelagic zone (200–1000 m; Figure 2). These strategies require different physiological specializations. The duration of a dive is determined by the amount of oxygen stored in their muscles, blood, and lungs to support aerobic metabolism, known as the aerobic dive limit (ADL). Deeper dives require a greater ADL compared with shallow dives because of the greater transit time needed to reach the bottom. An examination of diving behavior and physiological capacity of marine mammals suggests that mesopelagic and benthic foragers use more of their physiological capacity compared with epipelagic foragers. Given that more time is required to reach the bottom, mesopelagic and benthic foragers appear to maximize bottom time and spend more of their day actively foraging [11]. Thus, benthic species have a reduced ability to increase their foraging effort in times of nutritional stress. This impacts reproductive output, offspring growth, and survival. In addition, because adults of benthic-foraging species are working near their physiological limit, the juveniles with their reduced physiological capabilities and oxygen stores should be vulnerable to resource limitation. Survival of juveniles in benthic-foraging species might be a major determinant of demographic trends [12]. Benthic-foraging species might also be particularly sensitive to changes in their habitat resulting from climate change or interactions with fisheries, which remove the larger size classes of fish upon which they depend. Species such as Australian (*Neophoca cinerea*) and New Zealand (*Phocarctos hookeri*) sea lions, which specialize on benthic or demersal prey, have endangered populations, while the California sea lion (*Zalophus californianus*) a generalist that feeds on prey throughout the water column, is now thriving and has recovered from previous exploitation [12].

A conceptual framework for vulnerability quantification

These examples reveal how extinction risk is tied to degree of specialization in an intimate manner. While several ecological traits have been evaluated as potential correlates

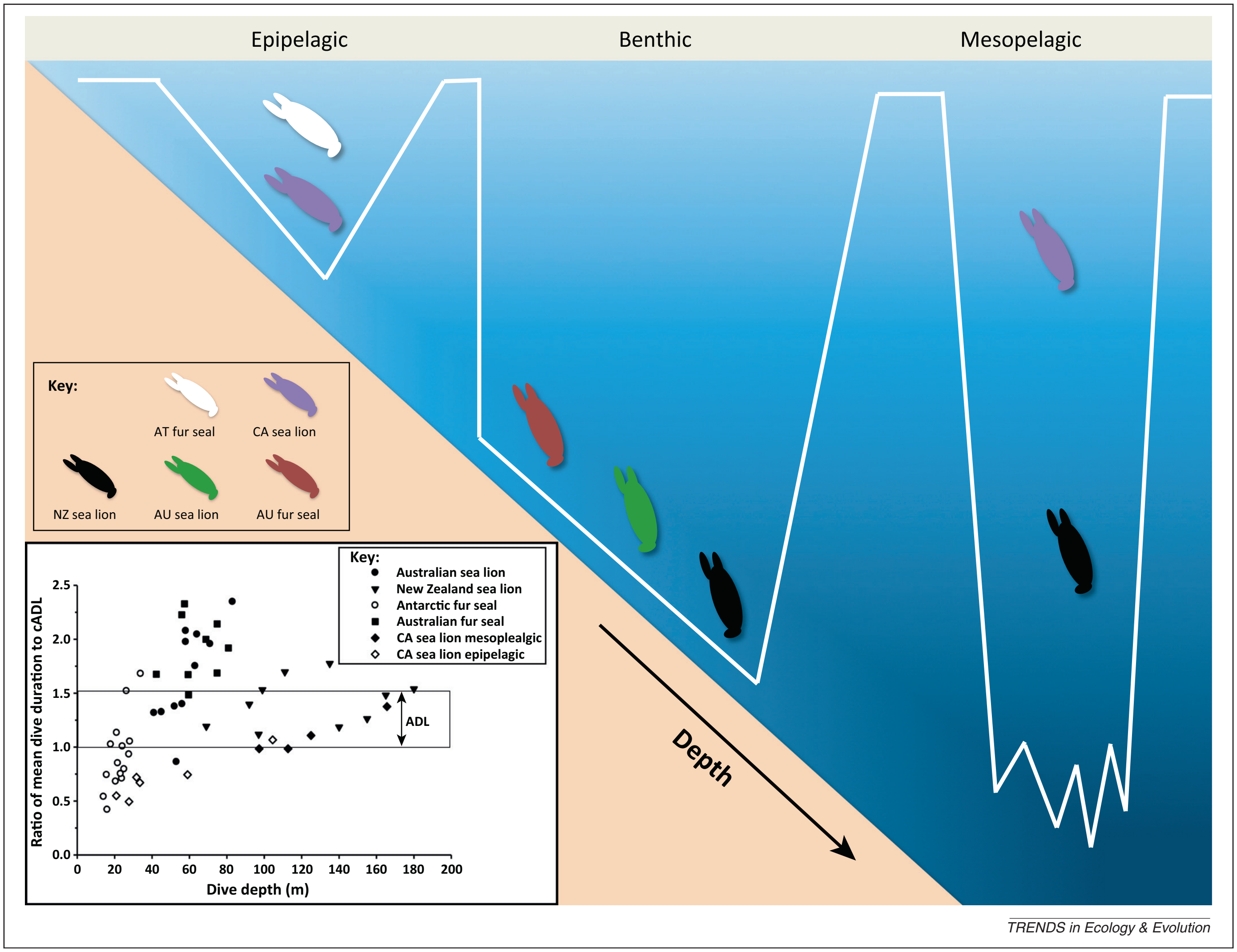

Figure 2. The threats to marine mammals are similar to other marine species and include, but are not limited to, fisheries bycatch, directed harvest, pollution, habitat loss, and climate change. Polymorphisms in foraging patterns highly interact with these threats. Epipelagic, benthic, and mesopelagic are three of the primary foraging modes that pinnipeds species exhibit. Inset: Diving performance defined as the ratio between average dive duration and the predicted aerobic dive limit as a function of dive depth in five pinnipeds species from [12]. Unfilled symbols represent epipelagic foragers (near surface), and filled symbols represent either benthic or mesopelagic foragers. With increasing depth, pinnipeds experience both increased physiological challenge and an increased investment in time needed to reach resources at depth. For those species that forage for nutrient-enriched demersal prey in benthic and mesopelagic habitats, there is inherent risk if these resources become suddenly depleted or overfished. Moreover, these strategies can also overlap with other fisheries, thus rendering species and individuals with enhanced diving abilities disproportionately vulnerable to bycatch. Reproduced, with permission, from [12].

of extinction risk [2], we suggest five quantifiable traits that are shared by almost all vertebrates and influence the ability to adapt to changing environmental conditions: (A) ecology (i = dietary breadth, ii = habitat specialization, iii = geographic range, and iv = population density); (B) morphology (i = body shape and ii = body size); (C) life history (i = fecundity, ii = age at maturity, and iii = maximum age); (D) behavior (i = mating strategy and ii = mode of foraging for food); and (E) physiology (i = stress response and ii = thermal tolerance). Population status may be included (population size and trajectory). These traits could be measured or aggregated, and then compared among species. Then, a standardized metric of specialization can be created that takes them all into account. One could then use these specialization values to estimate future extinction risk based on the premise that more specialized species, even if flourishing today, may be prone to human disturbance. By contrast, highly generalized species with low population estimates might be at a lower risk if they can exploit, for example, a wide range of habitats or food types.

Concluding remarks

Humans are the most prominent current evolutionary driver on Earth, yet conservation biologists continue to debate the proximate causes of extinction in animal and plant species. Here, we have provided a flexible framework and a proposed methodology that complements current methods for assessing extinction risk. More work is needed to operationalize our framework, but we hope that our paper reveals the benefits for managers and policy makers to work with ecologists and evolutionary biologists.

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