EVOLUTIONARY BIOLOGY

Fearful effects on ecological competitors

Predators are often thought to structure ecological communities by consuming competitively dominant species, which promotes the coexistence of species. But an alternative mechanism might involve the effects of fear. SEE ARTICLE P.58

OSWALD J. SCHMITZ

The Caribbean and its surrounding region harbour an incredible diversity of anole lizard species[1]. They come in many shapes and sizes, and occupy a variety of places in shrub and tree habitats. This separation in morphology and the use of space reflects the lizards' varied functional roles on the island and in the mainland coastal ecosystems that they inhabit[1]. For example, some green, small-bodied, short-limbed species of anole occupy the canopies of shrubs and trees, nimbly traversing twigs and branches to pluck insect prey[2]. Other, brown anole species perch lower down on the trunks, relying on their long, stocky legs to help them jump to the ground to sprint after insects[2]. There are numerous theories as to how such ecological and morphological diversity arises, and on page 58, Pringle *et al.*[3] present the results of a long-term field study into the effect of predators on anole lizards. Intriguingly, their conclusion is not one that would normally be considered in relation to the role of predators.

Explanations for how ecomorphological diversity, such as that seen among Caribbean species of anole, arises usually invoke the classical idea of adaptive radiation[1,4]. Here, close competitors diverge evolutionarily in terms of form and function (a process called niche divergence) to reduce overlap in the use of limiting resources. Accordingly, multiple species can coexist because they have complementary niches, with the exact number of coexisting species set by the breadth of each species' niche relative to the available resources. This explanation is intuitively satisfactory. But it leaves out a potentially important piece of the story, which has long been addressed by theory[5–8]: that predators might determine which species coexist, by mediating competitive interactions.

Predators are commonly thought to promote diversity if they preferentially consume the strongest competitor species. Such a consumptive effect relieves competitive pressure on other species, thereby enabling the coexistence of multiple species (Fig. 1a), and is well established as the keystone-predation effect[5–7]. However, more-recent thinking recognizes that predators can elicit a non-consumptive effect in their prey, namely, fear. The mere perception of a predation risk can cause prey to adaptively change their behaviour, morphology or physiology to alleviate the pressure of predation[9]. In particular, prey can take refuge in predator-free habitats[9,10], which could intensify the competition between species for particular territories and resources[8]. Known as refuge competition, this effect then disrupts coexistence, reducing diversity (Fig. 1b).

Pringle *et al.* offer a test of these alternative explanations that involves meeting the stringent evidentiary criteria needed to demonstrate niche-based coexistence. Foremost among these is the invasibility criterion, in which it must be shown that a competitor species can invade a community and increase its own abundance when already-resident competitors exist at their natural abundances[7,11]. In addition, the invading and resident competitor species must be shown to persist together by maintaining long-term positive fitness (the ability of individuals in a population to survive for long enough to reproduce)[7,11]. Finally, species must be shown to have complementary niches[7,11]. Meeting all these conditions is logistically challenging for any field study, because the criteria must be demonstrated across systematically replicated treatment conditions (communities of both invaders and residents) and control conditions (only residents), while also contending with background environmental variability.

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The authors' intrepid experiment involved 16 natural, tiny Caribbean islands. Each was already occupied by a species of trunk-inhabiting brown anole, *Anolis sagrei* — predicted (by dint of their previous occupation) to be the stronger competitor, which, without keystone predation, would preclude coexistence with other anoles (Fig. 1). To 12 islands, the investigators added factorial combinations of a canopy-dwelling green competitor, *Anolis smaragdinus*, and a predatory ground-dwelling, curly-tailed lizard species (*Leiocephalus carinatus*) that eats both insects and anoles. The remaining four islands were left as controls.

Under the control conditions, the resident

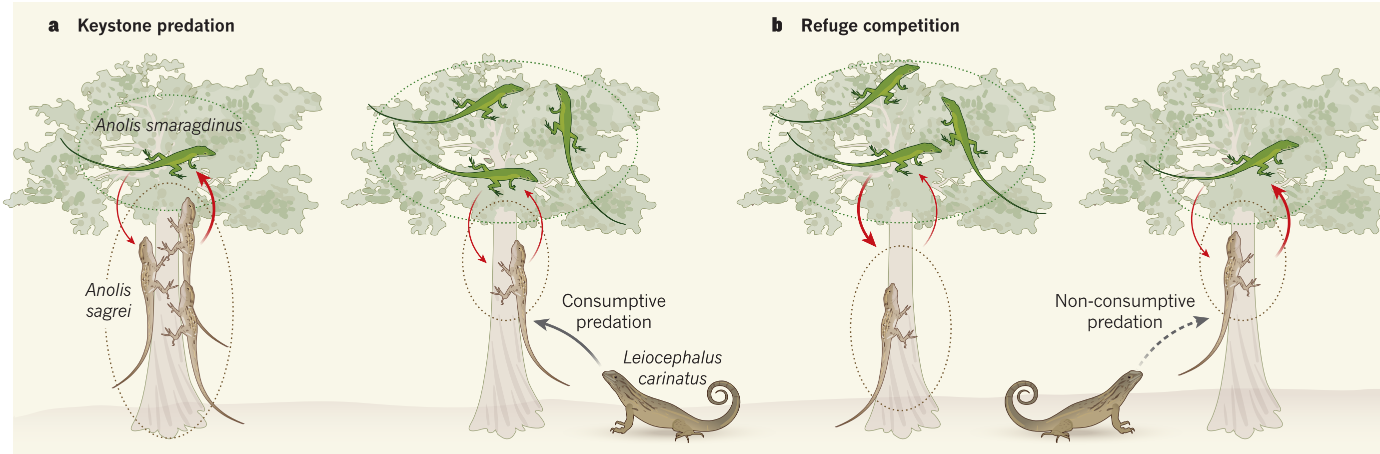

Figure 1 | Two ways in which an introduced predator might mediate the coexistence of competitive species. **a**, Brown anoles (*Anolis sagrei*) live on tree trunks and on the ground, whereas green anoles (*Anolis smaragdinus*) are largely arboreal. They compete for insect prey and, to a certain extent, for territory. Ovals depict the ranges of the two types of anole under various circumstances. Curly-tailed lizards (*Leiocephalus carinatus*) are ground-dwelling reptiles, and eat both anoles and insects. Pringle *et al.*[3] studied the effects of this predator on anole coexistence. Without predators, brown anoles competitively dominate green anoles (left, indicated by arrow thickness), which minimizes coexistence. A theory known as the keystone-predation effect proposes that the introduced predatory lizard would preferentially consume brown anoles (right), indirectly boosting the abundance of green anoles and promoting competitor coexistence. **b**, Pringle and colleagues' study supports the refuge-competition theory of coexistence. The authors observed that, without predators, brown and green anoles live in disparate locations and the green anoles competitively dominate the brown ones (left). Predator introduction had a non-consumptive effect: fear caused brown anoles to seek refuge higher up, which intensified competition with green anoles and thwarted coexistence (right).

brown anole had positive fitness for the six-year duration of the study. In the absence of predators, populations of invading green anoles underwent an average eightfold increase, thereby satisfying the invasibility criterion. Brown and green anoles persisted together, thereby satisfying the fitness criterion. Furthermore, the authors' exacting use of advanced DNA-based diet analysis revealed only limited similarity in the exploitation of insect prey by brown and green anoles, which affirmed that they coexisted through niche complementarity. But the idea that keystone predation could explain this coexistence began to unravel. It was the green, not the brown, anole that seemed to be the dominant competitive species, with the green anole instigating an approximately 50% reduction in the size of the brown-anole populations among replicate islands.

Moreover, the successful invasion of the predatory lizard further rearranged things in ways that would not be expected under the keystone-predation effect. The green-anole populations, especially, declined to about one-tenth of their abundance on predator-free islands, and those of brown anoles declined less so. In addition, half of the green-anole populations were put on a trajectory towards extinction rather than coexistence. Fascinatingly, the decline could not be attributed to a consumptive predator effect, given that the green anoles and the predatory lizard were segregated spatially, with the predators dwelling on the ground and the green anoles in the canopy. Further analyses revealed that the brown anoles relocated higher up the trunks and into the lower canopy to evade predation. This shift altered the competitive dominance in favour of brown anoles, and intensified competition for space and diet between brown and green anoles.

Although the ecological function of the brown anole had clearly changed, the authors did not explore whether its form had changed as well. That such a change can occur is demonstrated by a previously staged experimental invasion of a ground-dwelling predator[12], which induced a similar shifting of trunk-living anoles to the canopy. This relocation instigated an almost immediate developmental change from stocky to shorter, nimble limbs, relative to individuals on control islands, which facilitated active manoeuvring by the anoles on thin branches. Whether or not the refuge-competition mechanism that has been revealed by Pringle *et al.* can drive such adaptive morphological change in Caribbean anoles remains to be seen.

However, the unprecedented ecological realism of the authors' experiment offers convincing evidence that the concept of refuge competition should be entertained more seriously. It is a clear demonstration of one among several newly discovered, but until now untested, outcomes that were predicted by recent general theory on the myriad ways in which consumptive and, especially, non-consumptive predator effects can disrupt and promote prey coexistence[8,13]. The finding certainly changes how ecologists and evolutionary biologists should think about the processes that structure communities. In an era that has been dominated by people's alteration of ecological systems, such rethinking is sorely needed to anticipate the fate of communities when new predatory species invade. ■

Oswald J. Schmitz *is in the School of Forestry and Environmental Studies, Yale University, New Haven, Connecticut 06511, USA.*
e-mail: oswald.schmitz@yale.edu

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UPDATE

The News & Views 'Asian glaciers are a reliable water source' by Tobias Bolch (*Nature* **545**, 161–162; 2017) reported on a paper, 'Asia's glaciers are a regionally important buffer against drought' (H. D. Pritchard *Nature* **545**, 169–174; 2017), that was subsequently retracted. A revised version of the paper has now been published (H. D. Pritchard *Nature* **569**, 649–654; 2019). The News & Views still reflects the conclusions of the revised paper, except for one detail: annual melt from glaciers upstream of the Tarbela reservoir accounts for more than the total amount of the reservoir's storage volume, rather than two-thirds of the volume, as originally stated. The online version of the News & Views has been corrected accordingly. The author's contact details have also been updated.