Within-population variation in dietary traits: implications for vulnerability and impact of imperiled keystone predators

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Abstract. Within a population of apex predators, differences among individuals can influence both their ecological impact and their vulnerability to threatening processes. Our field studies on a large monitor lizard (Varanus panoptes) in the Australian wet–dry tropics show that diets shift seasonally and depend upon a lizard’s sex and body size. Individuals that had previously been recorded to consume frogs were most at risk following biological invasion by toxic cane toads (Rhinella marina), as were individuals with broad diets during the wet season. As a result, mortality of those individual predators likely reduced predation pressure on other taxa (invertebrates and reptiles) that were frequently consumed by the same lizards that ate frogs, but with less benefit for taxa (e.g., rodents) that were consumed by non-anuran-eating individuals within the predator population. In particular, individuals killed by cane toads often had consumed agamid lizards, a group whose abundance has been reported to increase due to toad-induced mortality of V. panoptes. To understand the vulnerability of apex predators, or the ecological consequences of their extirpation, we need to incorporate the role of variation among individuals in critical ecological traits.

Key words: biological invasion; diet; ectothermy; niche; reptile; trophic cascade.

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INTRODUCTION

In many ecosystems, apex predators play vital ecological roles via top-down regulation of species at lower trophic levels (Heupel et al. 2014, Wallach et al. 2015). As a result, extirpation of apex predators can induce trophic cascades, modifying abundances of smaller taxa (e.g., via mesopredator release: Letnic et al. 2009, Newsome et al. 2017) and changing the behavior of prey species, with ramifications for broader-scale ecological processes (e.g., Ripple and Beschta 2003, Letnic et al. 2012). Although the keystone role of apex predators has attracted increasing scientific interest (e.g., Ripple and Beschta 2003, Beschta and Ripple 2010), the role of individual variation in ecological traits within a population of apex predators has received less attention. Although many apex predators have broad diets at a population level, individuals often differ substantially in key ecological traits such as habitat use and diet (Zerba and Collins 1992, Pintor and Byers 2015, Costa-Pereira and Pruitt 2019). Such intraspecific variation may create differences in vulnerability to anthropogenic threats (e.g., Webb et al. 2005), and nonrandom mortality of this kind may affect the impact of a reduction in predator abundance on lower trophic levels (Svanbäck and Persson 2004, Pettorelli et al. 2011).

Most research on the ecological role of apex predators has focused on endothermic taxa, but ectotherms (e.g., pythons, crocodilians, komodo dragons) are important in many tropical
ecosystems (e.g., Shine et al. 1998, Nifong et al. 2015, Jessop et al. 2019). Because most ectotherms are ecologically independent from the time of hatching, a population typically contains free-ranging individuals of a wide range of body sizes; mean sizes of males and females can diverge dramatically (e.g., Pough 1980, Pettorelli et al. 2011). Differences in body sizes may engender divergence in trophic roles, with larger individuals focusing on larger prey types and sometimes, foraging in different ways in different habitats (e.g., Vincent et al. 2005, Vincent and Herrel 2007). Additionally, the low maintenance metabolic requirements of ectotherms facilitate niche specialization of subgroups within the population; for example, one sex may feed only at one time of year, on prey that are only available at that time, whereas the other sex feeds on prey available at other times (e.g., Goiran et al. 2013). Thus, ectothermic apex predators offer robust models to explore the ways in which predators lack an evolutionary history of exposure to the distinctive bufadienolide toxins of toads and are killed if they ingest a cane toad (Shine 2010). That vulnerability has caused rapid population declines (sometimes, of >90%) in marsupial quolls, freshwater crocodiles, blue-tongue skinks, and importantly, varanid lizards (e.g., Shine 2010, Brown et al. 2011). Mortality of varanids has caused trophic cascades, increasing the abundance of taxa previously consumed by these large lizards (Brown et al. 2011, Doody et al. 2013, 2017). However, we know very little about how an individual predator’s phenotype affects its vulnerability when toads invade an area, nor about the effect of toad-induced mortality on the ecological impacts of surviving predators.

We gathered data to fill these knowledge gaps in the course of fieldwork at a remote field site in northwestern Australia (Ward-Fear et al. 2016). In particular, we aimed to determine (1) seasonal patterns of prey consumption in a tropical apex predator; (2) whether an individual predator’s sex and body size influence its diet; and (3) whether an individual’s dietary habits influence its vulnerability to a novel threatening process (the cane toad invasion). If predator diets depend upon sex and/or body size, and also predict vulnerability to toad invasion, we can plausibly expect that nonrandom mortality of predators will differentially affect the trophic cascade induced by varanid mortality following the invasion of cane toads (Brown et al. 2011, Doody et al. 2013, 2015).

**Methods**

**Study system**

Widely distributed across tropical Australia, floodplain monitors (*Varanus panoptes*) are among the largest lizards worldwide (Fig. 1a). Males can attain body lengths to 2 m and can weigh up to 7 kg; females rarely exceed 1.2 m and 2.5 kg (Shine 1986b, Ward-Fear et al. 2016). These giant lizards eat a wide range of prey types, including carrion (Shine 1986b, Christian 1995, Shannon and Mendyk 2009). Varanids are among the largest and most abundant predators in the Australian wet–dry tropics, a region of highly seasonal rainfall. Precipitation is concentrated in a three-month “wet season” (January–March), whereas temperatures are high year-round (Shine and Brown 2008). Annual monsoonal rains inundate low-lying areas, creating ephemeral wetlands and hence generating strong temporal shifts in prey availability for a generalist forager. Radiotelemetric studies of *V. panoptes* show that some individuals in moist habitats remain active almost year-round, whereas conspecifics in more arid habitats aestivate during the long “dry season” (Christian 1995, Christian et al. 1995).

We used radio telemetry to study the ecology of *V. panoptes* (Ward-Fear et al. 2016). Animals were caught while they were foraging, fitted with VHF transmitters, and tracked regularly for up to three years (*n* = 165). We ascertained the cause of mortality (ingestion of cane toads vs. other causes, such as predation by pythons) for all recovered individuals (see Ward-Fear et al. 2016 for methods). The study was conducted at

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Fig. 1. (a) The yellow-spotted floodplain monitor (*Varanus panoptes*), an apex predator in northern Australia; (b) representative seasonal prey items of *V. panoptes* scored in scat analyses. Row 1 (L–R): two-lined dragon (*Diporiphora bennettii*); mulga snake (*Pseudechis australis*); and robust skink (*Ctenotus robustus*). Row 2: long-footed frog (*Cyclorana longipes*); pale field rat (*Rattus tunneyi*); and barramundi (*Lates calcarifer*). Row 3: cane beetle (*Lepidota squamulata*); grasshopper; and reptile eggs.
Oombulgurri, a 16,000-ha floodplain in the Kimberley region of tropical Australia (15°08’34.73" S, 127°52’36.08" E). Low-lying areas are surrounded by higher drier ground, creating a habitat mosaic in space as well as time.

The sex of varanid lizards is difficult to determine from external morphology, so we ran molecular tests using primers Ksex1 and Ksex3, originally developed for *Varanus komodoensis* (Halverson and Spelman 2002; for methodology, see Ward-Fear et al. 2018).

**Dietary analysis**

To analyze the seasonal diets of *V. panoptes*, we obtained scats from 2013 to 2015, either when handling lizards after capture, while we were measuring them and fitting them with transmitters (*n* = 70 scats), or opportunistically during radio telemetry fieldwork across the area (*n* = 47 scats). Scat analysis is ethically preferable to invasive procedures such as stomach-flushing. Varanid scats are easily recognizable, being larger than those of any other lizard in the region. The site also contains another medium-sized varanid species, *V. gouldii*, but these occur in different microhabitats and are far less common than is *V. panoptes* (*total n* = 23 vs. 165 lizards), and hence, all or almost all the scats we found in the field likely were produced by the latter species.

Upon collection, scats were refrigerated individually in plastic bags. They were then soaked in water and separated through a fine sieve to collect all solid objects, the remains of which were air-dried. We classified prey items to a minimum of class (in some cases, order), quantifying (1) presence/absence and (2) the total proportion of remains in each scat. Frog remains were inferred by the concurrent presence of a large proportion of scat that lacked identifiable remains and the presence of tiny invertebrate fragments (too small for goannas to eat; Christian et al. 1995). We then calculated the frequency of prey occurrence as the presence/absence in each scat, across the entire scat collection for any given season (see ‘Statistical analysis’ for designation of seasons).

**Statistical analysis**

Using JMP Pro 14, we analyzed these data to explore the influence of a lizard’s sex and body size (snout-to-vent length; SVL) on its prey preferences. For analysis of seasonal trends, we separated records into the three seasons of *V. panoptes* activity at our field site: buildup (October–December), wet season (January–April), and dry season (May–August; see Shine and Brown [2008] for further information). These lizards rely on freestanding water (and the resources associated with it); when this dries up at our field site, animals begin aestivation in burrows (usually from August to October; G. Ward-Fear, personal observation).

We ran multiple, full-factorial logistic regressions with sex, size, and season (and their interactions) as independent variables with prey group and in some cases prey item as the dependent variables. Some analyses included all scats (*n* = 117), and others were restricted to scats of known individuals (and hence, for which we knew attributes such as sex and body size). We used ANOVAs to compare the number of prey items and prey categories (prey diversity) between male and female lizards. In all analyses, any nonsignificant interactions were deleted, and main effects were recalculated.

**Results**

**Overall dietary composition**

Many scats contained the remains of multiple types of prey (average of 2.4 prey categories per scat, range: 1–6; Fig. 1b). In our total sample of 117 scats (51 from the buildup, 41 wet season, and 25 dry season), the most common prey types recorded were cane beetles (50% of scats), crawling insects (37%), grasshoppers (26%; all invertebrates combined 74%), reptiles (49%), frogs (28%), rodents (16%), and carrion (fish and feral horse 5%; other prey items 16%). These prey-type groups were used in our statistical analyses. Within most of those categories, a wide range of prey species were consumed (Table 1).

**Seasonal differences in dietary composition**

When lizards first emerged from their dry-season refuges and commenced foraging during the buildup (landscape dry, but with occasional rain), they fed almost exclusively on cane beetles (*Lepidiota squamulata*: 90% of scats; see Fig. 2). With the onset of heavy rains (wet season), the diet shifted to other invertebrates, frogs, and reptiles. With the cessation of rains, varanids switched across to foraging primarily on reptiles and rodents. The
lizards utilized carrion more frequently in the latter phases of their annual activity (Fig. 2). A chi-square contingency table analysis confirmed that the relative numbers of these prey types differed significantly among seasons (Table 2).

Counts of prey remains in scats reinforced these patterns. For example, scats that contained remains (heads) of cane beetles typically held many such fragments (mean = 11.1 beetles per scat, range = 1–40). Scats contained significantly higher prey diversity (number of prey categories per scat) in the wet season (mean = 3 categories, min = 1, max = 5) than in either the buildup (two categories, 1–5) or the dry season (two categories, 1–4; $F_{2,116} = 4.99, P = 0.0083$).

**Sex differences in dietary composition**

Based on 66 scats produced by animals of known sex (25 females and 41 males), the diets of males and females differed in several aspects. In general, prey diversity was higher in scats from female lizards than from males (mean F, three types; M, two types; $F_{1,65} = 7.87, P = 0.0067$), irrespective of season. The two sexes also differed in the way in which the diet shifted seasonally. In the buildup, female lizards consumed more frogs ($n = 31, df = 1, \chi^2 = 5.25, P = 0.022$), crawling invertebrates ($n = 29, df = 1, \chi^2 = 5.06, P = 0.025$), and other items (e.g., reptile eggs; $n = 31, df = 1, \chi^2 = 4.02, P = 0.045$) than did males. In the wet season, females consumed more cane beetles ($n = 27, df = 1, \chi^2 = 7.67, P = 0.0056$) and grasshoppers ($n = 27, df = 1, \chi^2 = 4.9, P = 0.027$). In the dry season, females ate more crawling invertebrates ($n = 7, df = 1, \chi^2 = 7, P = 0.082$) than did males. Despite these seasonal fluctuations in prey preference, in general females focused more on invertebrates.

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Table 1. Prey items recorded in scats ($n = 117$) of varanid lizards *Varanus panoptes* on a tropical floodplain in tropical Australia. Bold numbers indicate total counts for each prey group.

| Prey group       | Identified remains | No. of scats | Percentage of total | Species include                                      |
|------------------|--------------------|--------------|---------------------|------------------------------------------------------|
| Cane beetle      | 59                 | 50           | *Lepidiota squamulata* |
| Grasshopper      | 30                 | 26           |                      |
| Crawling invertebrates | 43   | 37           |                      |
| Frog (in stomach only) | 20   | 17           |                      |
| Beetle           | 29                 | 25           | *Helea* spp.; *Anoplognathus* spp. |
| Cockroach        | 15                 | 13           | *Asana* spp.        |
| Carrion beetles  | 2                  | 2            |                      |
| All insects      | 86                 | 74           |                      |
| Reptile          | 57                 | 49           |                      |
| Dragon spp.      | 14                 | 12           | *Amphibolurus gilbertii*; *Diporiphora bennetii* |
| Skink spp.       | 31                 | 26           | *Tiliqua scincoides intermedia* (1); *Ctenotus robustus* |
| Snake spp.       | 18                 | 15           | *Aspidites melanocephalus*; *Liasis childrenii*; *Pseudochis australis* (3) |
| Frog             | 33                 | 28           | *Litoria rubella*; *Cyclorana australis*; *Cyclorana longipes* |
| Rodent           | 19                 | 16           |                      |
| Carrion          | 6                  | 5            |                      |
| Fish             | 2                  | 2            | *Lates calcarifer*   |
| Hair of feral Horse | 3            | 3            | *Equus caballus*     |
| Other            | 19                 | 16           |                      |
| Crab, bivalve, mollusk | 5          | 4            |                      |
| Egg (reptile)    | 5                  | 4            |                      |
| Plant material   | 6                  | 5            |                      |
| Bird             | 3                  | 3            |                      |
| Insect cocoon    | 3                  | 3            |                      |

*Notes:* All items were identified to species level where possible. Prey was then grouped into ecologically relevant categories, and scats were assessed for the presence/absence accordingly. Multiple prey groups were present in every scat; hence, the percentage of total (percentage of scats containing that prey type) does not add up to 100.
Fig. 2. Proportion of varanid lizard scats containing specific types of prey, as a function of season (buildup, wet, and dry). Panels show (a) female lizards ($n = 25$; buildup 12, wet 11, and dry 2); (b) male lizards ($n = 41$; buildup 19, wet 16, and dry 6).

Table 2. Results of contingency table analyses of scat composition by prey group, across three seasons (buildup, wet, and dry).

| Prey group     | $n$ | df | $X^2$   | $P$ (Pearson) | Significant results                                      |
|----------------|-----|----|---------|---------------|----------------------------------------------------------|
| Cane beetles   | 117 | 2  | 61.165  | $<0.0001^*$   | Build up $>$ wet $>$ dry                                  |
| Reptile        | 117 | 2  | 8.57    | 0.0138*       | Build up $<$ (wet = dry)                                  |
| Grasshopper    | 117 | 2  | 17.883  | 0.0001*       | Wet $>$ (build up = dry)                                  |
| Frog           | 117 | 2  | 26.575  | $<0.0001^*$   | Wet $>$ (build up = dry)                                  |
| Rodent         | 117 | 2  | 14.476  | 0.0007*       | Dry $>$ (build up = wet)                                  |
| Carrion        | 117 | 2  | 0.582   | 0.7476        | Build up = wet = dry                                     |
| Other          | 117 | 2  | 4.676   | 0.096         | Wet $>$ (build up = dry; trend only)                      |

Notes: All scats were included in this analysis ($n = 117$). Statistically significant differences ($P < 0.05$) are denoted with an asterisk (*), and the final column explains the nature of the significant effect.
Determinants of dietary composition

Effects of body size on dietary composition

The recently captured varanids from which we obtained scats ranged in size from 175 to 635 mm snout-to-vent length (females 270–465 mm; males 175–635 mm), and 65–5050 g in mass (females 270–1205 g; males 65–5050 g). In logistic regressions with prey type as the dependent variable, larger lizards were more likely to have consumed rodents \( (n = 70, \, \chi^2 = 1, \, \chi^2 = 6.93, \, P = 0.009) \). A varanid’s body size also influenced the number of prey items per scat, with larger lizards producing feces that contained more cane beetles \( (F_{1,41} = 13.75, \, P = 0.0006) \), and larger varanids were more likely to contain snakes and dragons than skinks \( (n = 34, \, df = 2, \, \chi^2 = 8.65, \, P = 0.0013) \). However, there was no significant effect of predator size on the number of prey categories that we detected in scats.

Determinants of dietary composition

Are some of the effects of season, sex, and body size on diet (above) an artifact of correlations among these variables? For example, seasonal differences in sex ratios and body sizes, or sex differences in mean body size, might create correlations between diet and a trait with no functional link to foraging. To clarify interactions between body size, sex, and season, we included these factors (and their interactions) in a multiple logistic regression with “whether or not a lizard ate prey type X?” as the dependent variable. We then deleted all nonsignificant interaction terms and reassessed the main effects. In most cases, multiple factors affected diets. We provide statistical output and explanations of significant patterns in Table 3 but describe the most pertinent results below.

Whether or not a lizard consumed frogs was a function of season (eaten most often in the wet season; \( n = 66, \, df = 2, \, \chi^2 = 23.54, \, P < 0.0001 \)) and an interaction between season and sex (females ate more frogs in the buildup, both males and females ate equal numbers in the wet season, and males ate more frogs in the dry season; \( n = 66, \, df = 2, \, \chi^2 = 7.37, \, P = 0.025 \)), and interaction between sex and SVL (larger females and smaller males ate more frogs; \( n = 66, \, df = 1, \, \chi^2 = 3.88, \, P = 0.049 \)).

Reptiles were least abundant in varanid diets during the buildup \( (n = 66, \, df = 2, \, \chi^2 = 7.24, \, P = 0.027) \) and were exploited primarily by small females and large males \( (n = 66, \, df = 1, \, \chi^2 = 4.97, \, P = 0.026) \). An interaction between sex and season was significant in determining the species consumed \( (n = 41, \, df = 4, \, \chi^2 = 32.8, \, P < 0.0001) \). In the buildup, the only reptiles eaten by female varanids were skinks, whereas males ate skinks (55%), dragons (27%), and snakes (18%). In the wet season, females ate more skinks (78%) than dragons (22%), whereas males ate predominantly dragons (62%); skinks 25%, snakes 13%). In the dry season, females ate equal numbers of skinks and dragons, while the only reptiles eaten by males were snakes. Grasshoppers were consumed most frequently in the wet season \( (n = 66, \, df = 2, \, \chi^2 = 51.18, \, P < 0.0001) \), mostly by large females and small males \( (n = 66, \, df = 2, \, \chi^2 = 11.19, \, P = 0.0037) \). In contrast, crawling invertebrates were consumed heavily by females during the dry season \( (n = 66, \, df = 2, \, \chi^2 = 9.92, \, P = 0.007) \).

Intercorrelations between types of prey consumed

Patterns of consumption of these different prey types exhibited significant intercorrelations: That is, a lizard that ate one type of prey was more or less likely to eat specific other types of prey. For example, a scat that contained the remains of frogs was unlikely to also contain cane beetles \( (n = 117, \, df = 1, \, \chi^2 = 6.5, \, P = 0.012) \) or rodents \( (n = 117, \, df = 1, \, \chi^2 = 3.78, \, P = 0.05) \) but more
Table 3. Results of full-factorial logistic regression analyses with season (buildup, wet, and dry), lizard sex and size (snout-to-vent length), and interaction terms as determinants of prey consumption (n = 66 scats of identified lizards).

| Prey group | Sex | SVL | Season   | Sex × SVL | Sex × Season | SVL × Season | Sex × SVL × Season | Explanation of significant results |
|------------|-----|-----|----------|-----------|--------------|---------------|---------------------|----------------------------------|
| Cane beetle| NS  | NS  | 28.37; <0.001 | NS        | NS           | NS            | NS                  | BU > W > D                       |
| Grasshopper| NS  | NS  | 51.18; <0.0001 | NS        | 11.19; 0.0037 | 12.19; 0.0023  | NS                  | W > D > B                        |
| Frog       | 10.43; 0.0012 | NS  | 23.54; <0.0001 | 3.88; 0.049 | 7.37; 0.025 | NS            | NS                  | Highest in large F and small M |
| Reptile    | NS  | NS  | 7.24; 0.07    | 9.92; 0.007 | NS           | NS            | NS                  | D: F > M; BU and W: F = M         |
| Rodent     | 9.98; 0.0016 | NS  | 0.05         | NS        | NS           | NS            | NS                  | BU < (W = D)                      |
| Carrion    | NS  | NS  | NS          | NS        | NS           | NS            | NS                  | Highest in small F and large M  |
| Other      | NS  | NS  | NS          | NS        | NS           | NS            | NS                  | M > F                            |

Notes: Chi-squared values appear in normal type; P values appear in italics. For Sex, SVL, and Sex × SVL, df = 1; for Season, Sex × Season, SVL × Season, and Sex × SVL × Season, df = 2. Higher-order interaction terms were deleted if not significant (NS) and main effects were recalculated. Explanation of significant patterns is provided here and in the text. D, dry season; BU, buildup season; F, female; M, male; W, wet season.

likely to also contain reptiles (n = 117, df = 1, \( \chi^2 = 10.42, P = 0.0012 \)), grasshoppers (n = 117, df = 1, \( \chi^2 = 7.08, P = 0.008 \)), and carrion (n = 117, df = 1, \( \chi^2 = 3.96, P = 0.047 \)). That pattern of co-occurrence was not an artifact of seasonal shifts in the importance of various prey types. If we restrict analysis to single seasons, scats containing frogs were also more likely to contain reptile fragments (n = 41, df = 1, \( \chi^2 = 6.58, P = 0.01 \)) and carrion (n = 41, df = 1, \( \chi^2 = 3.42, P = 0.06 \)) but not rodents (n = 41, df = 1, \( \chi^2 = 4.44, P = 0.035 \)) during the wet season. In the dry season, there was a nonsignificant trend for frog-containing scats to also contain invertebrates (n = 25, df = 1, \( \chi^2 = 3.14, P = 0.07 \)). Overall, then, lizards that ate frogs also ate invertebrates, reptiles, and carrion, but not cane beetles or rodents (Fig. 3).

Dietary habits versus vulnerability to cane toads

Do data on diets of individual varanids allow us to predict which are most vulnerable to the toad invasion? If so, we might expect that toad-induced mortality during the wet season (the time of year when most frogs are consumed) would fall most heavily on lizards that had previously been documented to eat frogs. In a multiple logistic regression on wet-season data with “killed by eating invasive toad” as the dependent variable, and all prey categories as predictors, the only significant predictor was whether or not the lizard had been recorded to consume native frogs when captured earlier (9 of 18 frog eaters ate toads and died vs. 0 of 9 non-frogeaters; \( n = 18, \) df = 1, \( \chi^2 = 11.5, P = 0.0007 \)). Also, lizards that were recorded to have diverse diets at this time of year (more types of prey per scat) were also more likely to die from cane toads (n = 27, df = 1, \( \chi^2 = 6.54, P = 0.012 \)), irrespective of sex or size.

Lastly, varanids that died from cane toads had consumed dragon lizards early in the year, more often than had individuals that survived (n = 12, df = 1, \( \chi^2 = 9, P = 0.0027 \)).
DISCUSSION

Large varanid lizards are prominent predators on floodplains across tropical Australia, and the fatal poisoning of *Varanus panoptes* by invasive cane toads has induced powerful trophic cascades that have restructured riparian communities (Doody et al. 2013, 2015, Brown et al. 2013). Our data show that the diets of these giant lizards vary in complex ways both seasonally and as a function of predator phenotype (sex and body size). Individuals that fed on native frogs were (unsurprisingly) more likely to be killed by eating toxic cane toads. Because frog-eating individuals also ate some but not other prey types, we infer that this nonrandom mortality then affected levels of predation on other prey types also. For example, previous studies have reported an increase in the numbers of agamid (dragon) lizards following toad-induced declines of *V. panoptes* (Doody et al. 2009, 2017). In our study, the varanids killed by cane toads tended to be those that had eaten dragon lizards early in the dragon’s annual activity period. Hence, removing agamid-eating varanids may have enhanced the abundance of these smaller lizards, with strong flow-on effects for ecosystem dynamics (Doody et al. 2009, 2017). Overall, our study supports the hypothesis that niche differences among individuals within a population of apex predators (as a function of phenotypic traits such as sex and body size) can influence an individual’s vulnerability to a novel threat. In turn, that nonrandom vulnerability may affect other components of the ecosystem.

How general is this result? Although specific links between phenotypic traits and niche parameters will differ among systems—and even, change within a single population over time—intraspecific divergences in foraging locations, tactics, and prey types likely will occur in many species of apex predators. An extensive literature documents strong empirical links between phenotypes and niches (including food habits) within populations; for example, correlations between predator size and prey type are widespread in many predators (e.g., Shine et al. 1998, Webb et al. 2005); an individual’s behavioral profile (expression of boldness, aggression, and exploration) can also influence its diet (Costa-Pereira and Pruitt 2019). Likewise, sex-based differences in feeding habits are so consistent in some taxa that they have resulted in the evolution of sex differences in trophic

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**Fig. 3.** Proportion of varanid lizard scats that contained various prey types, as a function of whether or not that scat contained remains of frogs. The x-axis depicts prey groups (with sample sizes for each group; y = contained frogs, n = did not contain frogs). The y-axis shows the percentage of scats (from a total of 117) containing each type of prey.
morphology (e.g., Shine 1989). Clearly, the magnitude of intraspecific niche divergence may be decreased by factors such as sexual monomorphism, a limited range of body sizes within a population, a restricted diversity of available prey, or reliance on group rather than individual hunting (e.g., Shine and Wall 2007). Nonetheless, it will often be true that an individual's phenotype affects its prey use within as well as among populations. Future work could usefully examine repeatability of dietary choices in individuals within a population, an aspect that was not logistically possible in our own study.

Covariation between different dietary components also is widespread. If different assemblages of prey taxa occur in different places or vary in their vulnerability to different predator tactics (e.g., ambush vs. active searching), a predator that captures prey type X is likely to also find prey type Y, but not prey type Z. Heterogeneity in the distribution or catchability of alternative prey types across a mosaic habitat thus may generate variation in prey types among individual predators (e.g., Woo et al. 2008). That variation is likely to be linked to attributes of a predator's phenotype that influence its ability to find, overpower, and ingest specific prey types: That is, predators will specialize on prey types best-suited to their own foraging abilities. As a result, we expect natural selection to generate a match between a predator's phenotype and its diet (Van Valen 1965).

Intraspecific variation in diet also may often link to intraspecific variation in vulnerability to threatening processes. In the system that we studied, that link is direct: Individuals that fed on native anurans were more likely to later consume a fatally toxic anuran when it invaded the site (as predicted for another anuran-eating predator in this system also Webb et al. 2005). In other cases, the link may be indirect. For example, the larger sex may feed on different prey, and also be more heavily hunted by humans because its larger size provides a more valuable trophy, or supply of meat or leather (Shine 1986a, Packer et al. 2009). In the lace monitor (Varanus varius), larger individuals are more likely to attack (and be fatally poisoned by) cane toads than are younger conspecifics (Jolly et al. 2015). In other cases, culling by humans may fall more heavily on juvenile than on adult predators (Bonnet et al. 1999, Millar and Fryer 1999, Shine and Mason 2004). The same kind of nonrandom mortality with respect to phenotypic traits is common in natural mortality events also, as exemplified by studies on the effects of extreme weather conditions on natural populations (e.g., Brown and Brown 1998, Grant and Grant 2002, Ujvari et al. 2010, 2016). In any population where an individual's phenotype affects its diet or habitat use, nonrandom mortality with respect to that phenotypic trait will affect the broader ecological impact of that mortality.

Although logistically more difficult to quantify, it is likely that predator diets often are affected by behavioral as well as morphological diversity within a population (Zerba and Collins 1992). That is, some types of individuals target some types of prey. Anecdotal evidence for prey-type specialization by individual apex predators is abundant (e.g., Yeakel et al. 2009, Pintor and Byers 2015). In our study, despite both males and female varanids consuming many reptiles, only male varanids consumed snakes (perhaps because males tend to be larger and bolder than females, and thus more willing to engage with dangerous prey; Ward-Fear et al. 2018). In extreme cases, subsets of conspecifics within the same area forage on very different prey using very different methods (e.g., orcas: Ford et al. 1998, Saulitis et al. 2000). Self-evidently, that intraspecific divergence in diets translates into differences in vulnerability to threats of various kinds, and into the impact of those predator ecotypes on the broader biotic assemblages with which they interact.

In summary, previous research has identified the key role of apex predators in regulating ecosystems, but has tended to neglect the fact that even within a single predator population—and sometimes, within the lifetime of a single individual—patterns of niche occupancy may be too complex to be captured by a single average for the entire population. Often, such a population may consist of multiple subsets of individuals that rely to different degrees on different resources. By incorporating information on diversity at that fine-grained level, we can better understand the vulnerability and ecological impacts of apex predators, and how best we can manage those populations to maintain keystone species in the landscape.
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