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Diets of native and introduced apex predators in Hawai'i

Carolyn S. Mostello[A] *and Sheila Conant*[B,C]

[A]Massachusetts Division of Fisheries and Wildlife, 1 Rabbit Hill Road, Westborough, MA 01581, USA.
[B]Department of Biology, University of Hawaii – Manoa, 3663 Alani Drive, Honolulu, HI 96822, USA.
[C]Corresponding author. Email: conant@hawaii.edu

Abstract. We report here on the diets of four apex predators in Hawai'i: the native pueo or Hawaiian short-eared owl (*Asio flammeus sandwichensis*) and three introduced species, the barn owl (*Tyto alba pratincola*), the feral cat (*Felis catus*) and the small Indian mongoose (*Herpestes javanicus*). To better understand dietary relationships between these predators, we studied diet, focusing on areas where they occur together. We collected disgorged owl pellets, and cat and mongoose faecal scats from eight areas located on five of the main Hawaiian Islands and identified prey items to the lowest possible taxonomic level. All species consumed rodents, birds, and arthropods, and the mammal species also included plants in their diets. The two owl species and the cat preyed primarily on rodents, whereas small cockroaches predominated in the diet of the mongoose. Diets of the owl species and the cat, but not the mongoose, varied significantly between areas. Dietary overlap was highest between the pueo and the barn owl and lowest between the owl species and the mongoose. Although barn owls took more rats than pueo, there was no evidence that the two owl species partitioned house mouse prey by size. On islands where there are no mongoose, both owls took a greater proportion of large arthropods in their diet, suggesting that mongoose reduced the abundance of the arthropod species that owls commonly took. There was no significant difference in pueo diets before and after introduction of the barn owl.

Additional keywords: apex predators, barn owl, diet comparison, dietary overlap, feral cat, Hawai'i, Hawaiian short-eared owl, introduced predators, small Indian mongoose

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Introduction

Five apex predator species are present in terrestrial Hawaiian ecosystems: three bird and two mammal species. Two owl and one hawk species occur in the Hawaiian archipelago (Pratt *et al.* 1987): the endemic Hawaiian short-eared owl, or pueo (*Asio flammeus sandwichensis*), the endemic Hawaiian hawk, or 'io (*Buteo solitarius*), and the barn owl (*Tyto alba pratincola*), which was first introduced to the islands in 1958 (Thistle 1959). The hawk is found only on Hawai'i Island, whereas the two owl species are found in a variety of habitat types on all the main Hawaiian Islands, with the barn owl being the more abundant of the two. Pueo are found most often in open grassland or open scrub, while barn owls are more common in forested areas and even in residential neighbourhoods. The two mammal apex predators are also introduced, comprising the feral cat (*Felis catus*) and the small Indian mongoose (*Herpestes javanicus*) (Tomich 1986). The cat, which was probably first introduced ~230 years ago, is present on all the main islands in a variety of habitats, while the mongoose, which was introduced in 1883, also occurs in a diversity of habitats on several main islands, but not on Kaho'olawe, Kaua'i, Lana'i, or Ni'ihau (Tomich 1986). The four species are known to have some degree of dietary overlap (Tomich 1986; Snetsinger *et al.* 1994; Mostello 1996).

The primary objective of this study was to analyse pellets and scats to describe the diets of the four widely distributed apex predators, with an emphasis on selecting study areas where they are sympatric. We examined inter- and intraspecific variation in prey selection and quantified the presence of vertebrate prey in owl diets. We also took advantage of the variation in predator distribution on the different islands to examine the extent to which sympatry affects diets.

The data reported in this study were collected in 1993–95. Prey species and prey populations change dynamically with constant new introductions of insect species and irruptions of small mammals. Our results provide a historical snapshot of ecological interactions in Hawai'i. These interactions continue to change (e.g. the mongoose is now established on Kaua'i), because there will almost certainly be more introductions of insect prey, if not additional small mammal prey species in the future. In addition, this study provides quantitative and qualitative comparisons of diets of four of Hawai'i's five apex predator species, using data collected simultaneously and systematically over a wide range of habitats on all the main islands of the Hawaiian archipelago.

Status of the two owl species

The pueo is believed to be in decline due to loss of habitat and nest predation (Scott *et al.* 1986). The barn owl is of interest, not only because it is perceived to be effective in rat control, but also because predation by individuals or pairs can have dramatic effects on seabird colonies once the owls have discovered the abundant food resource. Declines in the number of sightings of pueo were noted beginning in the early 1900s (Henshaw 1902; Perkins 1903; Bryan 1933; Honolulu Audubon Society 1941; Scott *et al.* 1986). Because pueo population sizes have never been estimated, evidence for this decline is largely anecdotal, although on some islands it is supported by Christmas Bird Counts from the 1950s to the present (Mostello 1996). Beginning in the 1960s, reports surfaced of owl mortalities and 'sick' owls (mostly barn owls, but also pueo), especially along roadsides (Au and Swedberg 1966; Gassmann-Duvall 1988; Gassmann-Duvall and Telfer 1987).

Knowledge of the causes of apparent owl declines is incomplete. Trauma, disease, and pesticide poisoning were evaluated as sources of mortality (Gassmann-Duvall 1988; Aye *et al.* 1995; Work and Hale 1996), but results were inconclusive. Loss of open habitat in Hawai'i has been considerable, decreasing available foraging habitat for pueo. Nest predation by introduced mammals on the ground-nesting pueo has been documented (Bryan 1933; d'Arcy Northwood 1940; Snetsinger 1995), but its effect on population size is unknown.

Two sources of evidence suggest that owl mortalities may be related to food availability. First, Work and Hale (1996) determined that emaciation was the primary cause of death in 22% of 74 barn owls and one of five pueo for which cause of death was diagnosed, suggesting that these birds starved to death. Second, data collected on Kaua'i between 1991 and 1992 showed a peak in barn owl mortality between February and May (Telfer 1993), suggesting that mortalities could be related to fluctuations in prey abundance. There are infrequent mouse irruptions in beach, grassland, scrub and mesic forest areas that begin in March or April and end by November. It is not known if mouse populations show seasonal highs or lows.

Materials and methods

Collection and analysis of pellets and scats

Diet was investigated by examining prey remains found in regurgitated owl pellets and in cat and mongoose faecal scats. Because there is little seasonal variation in Hawaiian ecosystems and because we could not age samples, pellets and scats were collected throughout the period between September 1993 and October 1995. Search effort was similar in all sampling areas. Collection of owl pellets involved searching in roosting and nesting sites or under perches in known or likely owl habitat. Cat and mongoose scats were collected only from areas where owl pellets were found. Pellets and scats were put in separate resealable plastic bags at the time of collection, and were air-dried upon return from the field. Pellets and scats were attributed to a predator species based on size, shape, and colour (Tomich 1971; Snetsinger *et al.* 1994; Mostello 1996), as well as their occurrence at known owl nest or roost sites.

Barn owl (Tytonidae) and pueo (Strigidae) pellets can be distinguished by shape, colour and size (Mostello 1994; Snetsinger *et al.* 1994). Barn owls are larger than pueo. We examined study skins at the Bishop Museum, and found that barn owl study skins averaged 338 g ($n = 5$), and pueo study skins averaged 260 g ($n = 8$). Barn owl pellets are rounder and wider than pueo pellets, flattened in one dimension, and often a glossy black compared with pueo pellets, which are more cylindrical than barn owl pellets (Mostello 1994). In pueo pellets prey bones tend to be aligned along the longitudinal axis of the pellet, whereas bones in barn owl pellets are randomly arranged. However, since there is some overlap in size and variation in shape between pellets of the two species, pellets that could not be assigned to one or the other owl species were not included in the analysis.

Cat and mongoose scats are readily distinguished by size (cat scats are larger), and colour (cat scats tend to be whitish). Also, cat scats are often 'pinched' at the ends and along the length of the scat. As cat faeces from one defaecation are frequently composed of several separate segments these segments were grouped as one scat.

After air-drying, owl pellets were either soaked overnight in water, then teased apart with forceps or they were gently broken apart, soaked, and occasionally stirred over a period of 2–4 h (depending upon size, density, and freshness of pellets and scats) in a solution of 100 g solid NaOH dissolved in 1 L water ($n = 300$) (modified from Schueler 1972). The solution was then rinsed through a 1 × 1 mm metal mesh strainer to extract prey fragments (limb bones, skulls, mandibles, and arthropod parts). The minimum number of vertebrate prey items per pellet was estimated by counting unique limb bones and mandibles. Using pellet data from several areas, we investigated whether the mean number of vertebrate prey individuals per pellet was correlated with the frequency of occurrence of prey (the fraction of all individual pellets and scats in which a prey taxon occurs). Numbers of arthropod individuals in pellets could not be determined as parts were extensively fragmented.

Preliminary analysis showed that occasionally no bones or hard parts were found in cat or mongoose scats. For this reason, scats were dissected dry, prey items and presence of feathers and fur were recorded, and the contents were then treated with NaOH, as described above, to dissolve the fur/hair. Numbers of mammal, bird, and arthropod individuals in scats could not be determined due to partial digestion of bone and extensive fragmentation of hard parts.

Although the three rat species (*Rattus exulans*, *R. norvegicus* and *R. rattus*) present in Hawai'i can be distinguished by skull characteristics (King 1990), rats in this study were not identified to species because few skulls were found in samples. Rats were distinguished from the house mouse (*Mus musculus*) on the basis of size and other characteristics of bones (King 1990; Mostello 1996). Birds and arthropods were identified to the lowest possible taxon using reference collections from the Bernice P. Bishop Museum, Honolulu, Hawai'i, USA.

Comparison of diets

To compare diets between species or areas, the null hypothesis that there was no difference in the proportions of prey items in diets was tested using Chi-square analysis. Due to extensive fragmentation and partial digestion of dietary items, particularly arthropods and particularly in scats, it was not possible to accurately express prey as a percentage of volume, weight, or number of prey items for all predator species. Therefore, Chi-square analysis was based on the occurrence of five designated prey categories. Multiple individuals of the same prey category in a single pellet or scat were treated as only one occurrence of that category. The five prey categories used in this analysis comprised rats, mouse, birds, arthropods and plants.

Pellets and scats were collected from a total of eight different areas on five islands. The size of collections was sometimes small or none, which limited statistical analyses to areas with collections of 20 or more pellets or scats, respectively, for the two owl species and the mongoose. Adequate samples for barn owls and mongoose were collected in all eight or six (mongoose are not present on Lana'i and Kaua'i) areas, but short-eared owls yielded fewer than 20 samples in four of the eight areas. Due to difficulty obtaining cat scats, two smaller cat scat collections ($n = 11$ and $n = 17$) were added for use in analyses. The areas were described by Mostello (1996) and include: (1) Hakalau Forest National Wildlife Refuge, Hawai'i Island (Hakalau); (2) Holei Pali, Hawai'i Island; (3) Palawai Basin, Lana'i (Lana'i); (4) between Ho'olehua and Mo'omomi Dunes, Moloka'i (E. Mo'omomi); (5) Moloka'i Ranch Wildlife Conservation Park, Moloka'i (WCP); (6) Lualualei Valley, O'ahu (Lualualei); (7) Kahe Point, O'ahu (Kahe Pt): (8) Lihu'e Airport area, Kaua'i (Kaua'i). When comparing diets of owls on mongoose-free (Kaua'i and Lana'i) and mongoose-occupied islands, pellets from all areas were used in analysis.

Fourteen pueo pellets collected on O'ahu in 1956 and stored at the Bernice P. Bishop Museum, Honolulu, were also analysed to examine whether they differed in prey composition from modern pellets.

Resource partitioning among owls by prey size

We addressed the question of whether the pueo and barn owl partition prey by size by comparing the size of *M. musculus* in owl pellets. Collection sizes of rat and bird remains were too small from any one area for analysis. Because in *M. musculus* mandible length and body length are correlated (Mostello 1996), we used lower right mandibles extracted from pellets as indicators of body size. Because mean body size of mice may differ among areas, each of four areas (Hakalau, Lualualei, Kaua'i, and Lana'i) where owl species co-occurred was considered separately, and data were analysed using a General Linear Model ANOVA (Minitab 8.2: Minitab Inc. 1991).

Dietary overlap

For comparison, dietary overlap was examined using both the Morisita–Horn index (Horn 1966):

$$R_0 = 2\frac{\sum p_{ij}p_{ik}}{\left(\sum p_{ik}^2 + \sum p_{ij}^2\right)}$$

and the Schoener index (1970):

$$Ro = 1 - 0.5\sum |p_{ij} - p_{ik}|.$$

In these equations, p_{ij} and p_{ik} stand for the proportions of prey item i in the diets of predators j and k, respectively. Both indices yield values ranging from zero (indicating no overlap in resource use) to 1.00 (indicating complete overlap). Langton (1982) considered values of 0–0.29 as 'low' overlap, 0.30–0.59 as 'medium' overlap, and 0.60 and above as 'high' overlap. It is in this 0.60 to 1.00 range that competition is thought to occur when resources are limited (Zaret and Rand 1971).

The 11 dietary categories used in these resource overlap equations were rat, mouse, bird, plant, small (<2 cm body length) cockroaches (*Pycnoscelus indicus*, possibly *Diploptera punctata*), a katydid (*Euconocephalus nasutus*), a cricket (*Gryllus bimaculatus*), other large (≥3 cm body length) Orthoptera, praying mantises (*Hierodula patellifera*, *Orthodera burmeisteri*, possibly *Tenodera angustipennis*), a centipede (*Scolopendra subspinipes*), and 'other prey/unidentifiable' (prey items which could not be identified, or occurred in extremely low numbers (only one or two individuals). For example, lizards and molluscs were found in a barn owl pellet and mongoose scats, and a mongoose scat respectively, but the diversity of species in these groups in Hawai'i makes specific identification difficult.

Randomisation tests

We compared dietary overlap among areas with varying numbers of predator species. At two areas (Lana'i and Kaua'i), the mongoose was absent, and at another area (E. Mo'omomi), pueo were either absent or very rare. Of the 16 dietary overlap values generated, nine occurred at areas in which only three predator species were present and seven when four or five predator species were present. Five were present at Hakalau due to the presence of the Hawaiian hawk. Because data in the form of overlap values are not independent, randomisation tests (see Edgington 1987) were used to test for significance of differences in overlap. Using Minitab 8.1 Accelerated (Minitab Inc. 1991), we performed 1000 permutations on the 16 overlap values to test the hypothesis that mean dietary overlap when there are only three predators is greater than would be expected if nine overlap values were drawn randomly from the pool of 16 values.

Results

All four predator species took individuals of the four dietary categories of rats, mice, birds, and arthropods (Table 1). The cat and mongoose also consumed plant material. For all areas combined, the mouse was equally common in diets of the two owl species and the cat (72–79% of pellets or scats), and was the most frequently occurring prey item in the diets of these species. However, the mouse was found in only 37% of mongoose scats. Rats were most common in barn owl (41%) and cat (37%) pellets and scats and were rare in mongoose scats (3%). Birds also were rare in the mongoose diet (3%), and most common in the cat diet (37%). Arthropods were most frequently found in mongoose (93%) and cat (69%) scats. Fig. 1 shows frequency of occurrence of five prey categories in the diets of the four species.

The introduced zebra dove (*Geopelia striata*) was the most common bird species found in pueo pellets, which contained no identifiable native bird remains (Table 1). However, ~15% of bird prey in pueo pellets was of juveniles, which precluded

Table 1. Numbers of owl pellets or mammal scats in which each prey type occurred
Numbers in parentheses are percentages

Prey type	Pueo ($n = 211$)	Barn owl ($n = 518$)	Cat ($n = 87$)	Mongoose ($n = 73$)
Mammals				
Mus musculus	154 (73.0)	409 (79.0)	63 (72.4)	27 (37.0)
Rattus spp.	37 (17.5)	212 (40.9)	32 (36.8)	2 (2.7)
Birds				
Carpodacus mexicanus (house finch)	1 (0.5)	2 (0.4)	–	–
Chasiempis sandwichensis (‘elepaio)[A]	–	1 (0.2)	–	–
Geopelia striata (zebra dove)	36 (17.1)	6 (1.2)	–	–
Hemignathus munroi (‘akiapola‘au)[A]	–	1 (0.2)	–	–
Hemignathus virens (‘amakihi)[A]	–	2 (0.4)	–	–
Himatione sanguinea (‘apapane)[A]	–	5 (1.0)	–	–
Leiothrix lutea (red-billed leiothrix)	–	1 (0.2)	–	–
Myadestes obscurus (‘oma‘o)[A]	–	3 (0.6)	–	–
Passer domesticus (house sparrow)	–	1 (0.2)	–	–
Streptopelia chinensis (spotted dove)	2 (0.9)	2 (0.4)	–	–
Vestiaria coccinea (‘i‘iwi)[A]	–	6 (1.2)	–	–
Zosterops japonicus (Japanese white-eye)	1 (0.5)	1 (0.2)	–	–
Unidentified Drepanidini spp.[A]	–	2 (0.4)	–	–
Unidentified Estrildidae spp.	1 (0.5)	3 (0.6)	–	–
Unidentified Phasianidae sp.	1 (0.5)	–	–	–
Other unidentified birds	25 (11.8)	28 (5.4)	32 (36.8)	2 (2.7)
Reptiles				
Anolis carolinensis	–	–	–	1 (1.4)
Unidentified Gekkonidae or Iguanidae spp.	–	1 (0.2)	–	1 (1.4)
Fish				
Tilapia spp.	–	–	–	2 (2.7)
Molluscs				
Unidentified sp.	–	–	–	1 (1.4)
Arthropods				
Chilopoda				
Scolopendra subspinipes	–	–	8 (9.2)	11 (15.1)
Coleoptera				
Aphodius lividus	–	–	1 (1.1)	–
Callosobruchus sp.	–	–	1 (1.1)	–
Notiobia purpurascens	–	–	–	1 (1.4)
Unidentified coleopteran larvae	–	–	–	1 (1.4)
Hymenoptera				
Camponotus variegatus	–	–	–	1 (1.4)
Lepidoptera				
Agrius cingulata	–	–	1 (1.1)	–
Ascalapha odorata	–	–	1 (1.1)	–
Unidentified Lepidoptera spp.	–	–	1 (1.1)	1 (1.4)
Orthoptera				
Euconocephalus nasutus	35 (16.6)	108 (20.8)	29 (33.3)	8 (11.0)
Gryllus bimaculatus	29 (13.7)	21 (4.1)	24 (27.6)	–
Oedaleus abruptus	–	–	2 (2.3)	–
Periplaneta spp.	–	2 (0.4)	1 (1.1)	3 (4.1)
Schistocerca nitens	5 (2.4)	–	6 (6.9)	5 (6.8)
Small ($\sim$2 cm body length) cockroaches[B]	4 (1.9)	3 (0.6)	14 (16.1)	63 (86.3)
Praying mantids[C]	14 (6.6)	23 (4.4)	2 (2.3)	23 (31.5)
Unidentified Orthoptera spp.	–	1 (0.2)	1 (1.1)	4 (5.5)
Other unidentified arthropods	10 (4.7)	1 (0.2)	4 (4.6)	5 (6.8)
Plants (all are seeds except where indicated)				
Asteraceae				
Bidens pilosa	–	–	1 (1.1)	–
Chenopodiaceae				
Chenopodium sp.	–	–	1 (1.1)	–

(*Continued*)

Table 1. (Continued)

Prey type	Pueo (*n* = 211)	Barn owl (*n* = 518)	Cat (*n* = 87)	Mongoose (*n* = 73)
Fabaceae				
cf. *Desmodium*	–	–	4 (4.6)	–
cf. *Leucaena leucocephala*	–	–	1 (1.1)	–
Unidentified Fabaceae sp.	–	–	–	1 (1.4)
Malvaceae				
cf. *Malvastrum*	–	–	3 (3.4)	–
Poaceae				
cf. *Panicum*	–	–	1 (1.1)	–
cf. *Triticum*	–	–	4 (4.6)	–
Unidentified grass blades	–	–	8 (9.2)	–
Phytolaccaceae				
Rivina humilis	–	–	1 (1.1)	–
Unidentified seeds	–	–	5 (5.7)	6 (8.2)
Indigestible items				
Glass	–	–	2 (2.3)	–
Paper	–	–	1 (1.1)	–
Plastic	–	–	3 (3.4)	–
Other				
Eggshell (unknown origin)	–	–	2 (2.3)	3 (4.1)
Unidentifiable item	1 (0.5)	–	1 (1.1)	1 (1.4)

[A]Native species.
[B]*Pycnoscelus indicus*, possibly *Diploptera punctata.*
[C]*Hierodula patellifera*, *Orthodera burmeisteri*, possibly *Tenodera angustipennis.*

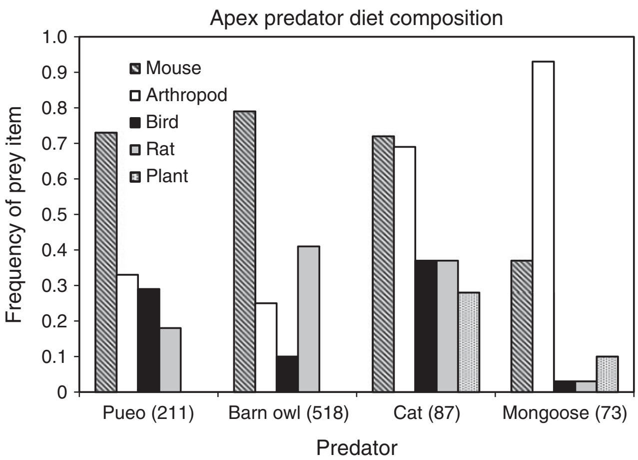

Fig. 1. Frequencies of occurrence of major prey items in diets of owls, cats and mongooses. Sample sizes are shown in parentheses.

allocation to species on the basis of bone identification. The barn owl took a wider variety of bird species than did the pueo (Table 1), including several species of Hawaiian honeycreeper (Fringillidae: Drepanidini) at one area (Hakalau), one of which was identified as the endangered 'akiapola'au (*Hemignathus munroi*). Approximately 30% of bird remains in barn owl pellets was of juveniles. On the basis of the size of bone specimens, we suspect that substantial juvenile material from Hakalau represented honeycreepers.

Insect remains in pellets of the two owl species were of large species (≥3 cm body length) with the exception of a few small cockroaches (*P. indicus*, <2 cm body length). *E. nasutus* and, to a lesser extent, *G. bimaculatus* dominated the arthropod component of diets of the two owl species (Table 1). Remains of a small lizard (Iguanidae or Geckkonidae) were found in one barn owl pellet. Although seeds occurred in owl pellets, they were always associated with granivorous birds, and therefore were not considered owl food items.

The cat and mongoose consumed a greater diversity of arthropods than did owls, and arthropod remains also occurred more frequently in cat and mongoose scats than in owl pellets (Table 1, Fig. 1). Small cockroaches, particularly *P. indicus*, dominated the insect portion of the mongoose diet, and were found in 86% of scats. While we were unable to systematically quantify the volume of each dietary category in pellets and scats, we noted that 48% of mongoose scats were composed entirely of arthropod remains. The most abundant arthropod in the cat diet was *E. nasutus*, although *G. bimaculatus* was also common, as was the case in diets of the two owl species. Some plant material in cat and mongoose scats may have been incidentally ingested while grooming, or ingested, with bird prey in the case of the cat as 42% of cat scats containing seeds also contained bird (including seed eaters) remains. Occasional eggshell fragments were found in cat and mongoose scats, together with fish (*Tilapia* spp.) and small lizards (Iguanidae or Geckkonidae) in mongoose scats, and artificial items (glass, plastic and paper) in cat scats (Table 1).

Comparative analysis of diets

Diets were different between the four collection areas with sufficient data for both owl species and the cat (pueo: $\chi^2 = 105.77$, d.f. $= 9$, $P < 0.0005$; barn owl: $\chi^2 = 201.92$, d.f. $= 21$, $P < 0.0005$; cat: $\chi^2 = 25.84$, d.f. $= 12$, $P = 0.01$)

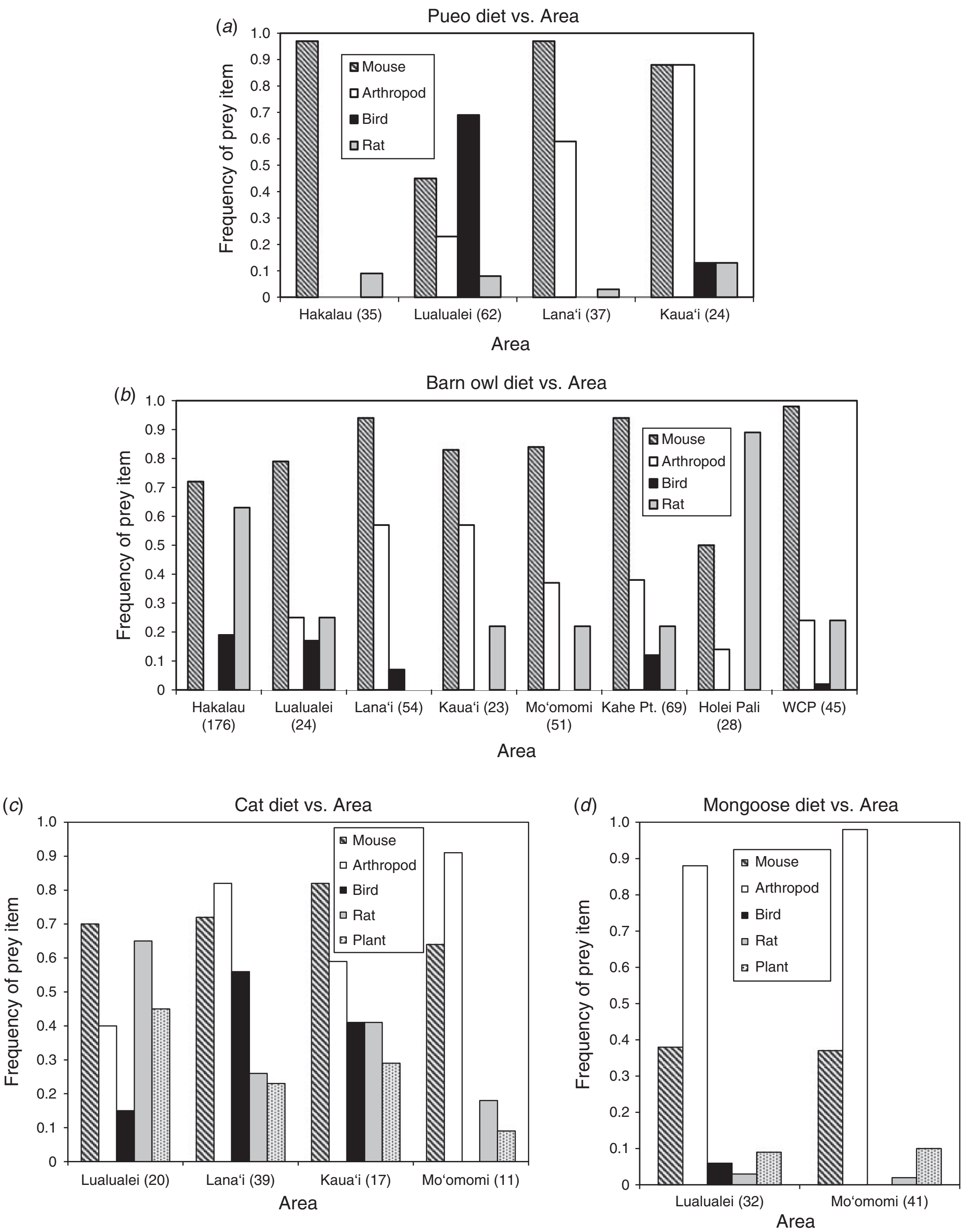

Fig. 2. Frequencies of occurrence of major prey items in predator diets between areas. (*a*) Pueo; (*b*) barn owl; (*c*) cat; (*d*) mongoose. Sample sizes are shown in parentheses.

(Fig. 2*a*–*c*). In contrast, mongoose diets did not differ significantly ($\chi^2 = 2.79$, d.f. $= 4$, $P = 0.59$) between the two areas with sufficient data for this species (Fig. 2*d*). Mean numbers of vertebrate prey individuals per pellet (Table 2) and frequency of occurrence between areas were positively correlated for both the pueo ($r = 0.99$ [rat], 0.90 [mouse], 1.00 [bird]; $n = 4$ areas) and barn owl ($r = 0.98$ [rat], 0.78 [mouse], 0.89 [bird]; $n = 8$ areas). This indicates that higher frequencies of occurrence reflect greater numbers of prey individuals (and thus elevated importance) in the diet.

Table 2. Mean numbers of vertebrate prey items per owl pellet
Standard deviations are shown in parentheses

Area	Barn owl pellets				Pueo pellets			
	Rat	Mouse	Bird	*n*	Rat	Mouse	Bird	*n*
Hakalau	0.77 (0.67)	2.17 (2.11)	0.35 (0.84)	161	0.09 (0.28)	3.60 (1.79)	–	35
Lana'i	–	2.91 (1.72)	0.07 (0.26)	54	0.03 (0.16)	2.49 (1.48)	–	37
Kaua'i	0.26 (0.54)	1.83 (1.64)	–	23	0.13 (0.34)	2.67 (2.01)	0.17 (0.48)	24
Lualualei	0.33 (0.64)	2.25 (1.73)	0.17 (0.38)	24	0.09 (0.29)	1.07 (1.67)	0.87 (0.75)	55
E. Mo'omomi	0.25 (0.52)	2.14 (1.50)	–	51	–	–	–	–
Kahe Pt	0.15 (0.42)	5.59 (2.26)	0.05 (0.31)	41	–	–	–	–
Holei Pali	1.50 (0.91)	0.77 (1.23)	–	22	–	–	–	–
WCP	0.27 (0.50)	4.29 (2.20)	0.02 (0.15)	45	–	–	–	–
All areas	0.50 (0.68)	2.57 (2.25)	0.15 (0.55)	421	0.18 (0.41)	2.12 (1.90)	0.34 (0.63)	151

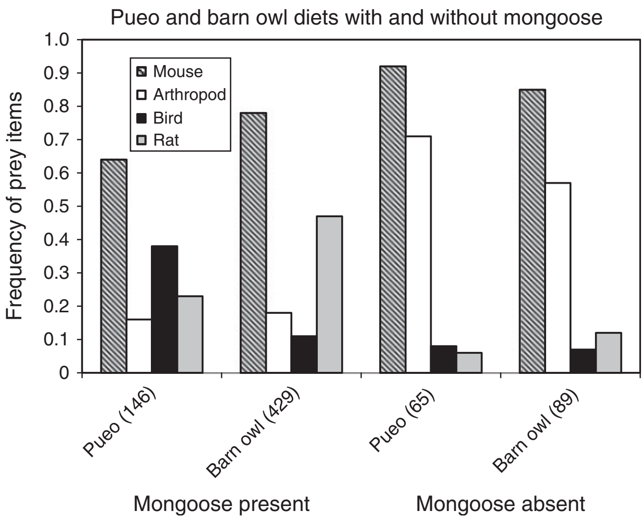

Fig. 3. Frequencies of occurrence of major prey items in owl diets at mongoose-occupied and mongoose-free areas. Sample sizes are shown in parentheses.

To examine dietary relationships between the two owl species, we compared their diets from four areas where they co-occurred and where sufficient data were obtained for analysis. At Hakalau and Lualualei, diets of the pueo and barn owl were significantly different from each other ($\chi^2 = 26.42$, d.f. $= 2$, $P < 0.0005$, and $\chi^2 = 16.34$, d.f. $= 3$, $P = 0.001$, respectively). In contrast, on Lana'i and Kaua'i, diets of the pueo and barn owl were not significantly different ($\chi^2 = 4.23$, d.f. $= 3$, $P = 0.24$, and $\chi^2 = 4.13$, d.f. $= 3$, $P = 0.25$, respectively). Using data from all four areas (Fig. 3), diets of the pueo and barn owl were significantly different from each other in mongoose-occupied areas ($\chi^2 = 64.46$, d.f. $= 3$, $P < 0.0005$), but not in mongoose-free areas ($\chi^2 = 2.28$, d.f. $= 3$, $P = 0.52$). Notably, arthropods were much more common in pellets of both owl species from mongoose-free areas than from mongoose-occupied areas. It should be noted that the high occurrence of bird prey in pueo diets from mongoose-occupied islands is strongly influenced by a large collection size from Lualualei, where the zebra dove, a small, slow-moving ground feeder, is extremely common. Similarly, the high occurrence of rats in the barn owl diet on mongoose-occupied islands is strongly influenced by a large collection from Hakalau, where rats exist in extremely high densities (Smith and Fancy 1998). Pueo diet as determined from pellets collected in 1956 (prior to introduction of the barn owl) was not significantly different from pueo diet in this study ($\chi^2 = 5.00$, d.f. $= 3$, $P = 0.17$).

Dietary overlap and randomisation tests

The Morisita–Horn index generally yielded higher overlap values than did the Schoener index (Table 3). Dietary overlap between the barn owl and pueo was high (0.55–0.97), overlap between the two owl species and the cat was medium or high (0.51–0.80), overlap between the two owl species and the mongoose was medium or low (0.24–0.39), and overlap between the mongoose and cat was medium or high (0.45–0.78).

Randomisation tests showed that overlaps between predators were significantly higher than expected when only three potential competitors were present at an area (E. Mo'omomi, Lana'i, Kaua'i) as opposed to the presence of four (Lualualei) or five (Hakalau) potential competitors. Only 28 of 1000 means ($P = 0.028$) randomly generated from Schoener index data and 29 of 1000 means ($P = 0.029$) generated from Morisita–Horn index data were greater than, or equal to, the observed means.

Discussion

Predator diets

Pueo and barn owl

The proportions of pueo prey categories found in our study were similar to those reported by Snetsinger *et al.* (1994) from 36 pueo pellets collected from Hawai'i Island, Kaho'olawe (not included in our study) and Kaua'i. In contrast, Schwartz and Schwartz (1951) found only rodent remains in 75 pueo pellets, although this result could have reflected a rodent population irruption or a restricted collection area (the area was not stated). The primary difference between pueo diet in 1956, before barn owl introduction(s) and this study was that birds decreased and arthropods increased in importance in our 1993–95 collections, although differences were not significant. Although it is possible that barn owls may occasionally take pueo nestlings, the introduction of the barn owl does not appear to have had an

Table 3. Morisita–Horn (Horn 1966) and Schoener (1970) dietary overlap values for different predator pairs between areas
Schoener values are shown in parentheses. P, pueo; B, barn owl; C, cat; M, mongoose

Area	Island	B × P	B × C	B × M	P × C	P × M	C × M
Hakalau[A]	Hawai'i	0.74 (0.55)	–[B]	–[B]	–[B]	–[B]	–[B]
Lualualei	O'ahu	0.69 (0.56)	0.76 (0.57)	0.34 (0.24)	0.53 (0.51)	0.27 (0.28)	0.47 (0.45)
E. Mo'omomi[C]	Moloka'i	0.69 (0.51)	0.39 (0.32)	–	–	–	0.78 (0.63)
Kaua'i[D]	Kaua'i	0.93 (0.75)	0.77 (0.57)	–	0.80 (0.61)	–	–
Lana'i[D]	Lana'i	0.97 (0.86)	0.73 (0.55)	–	0.71 (0.56)	–	–

[A]Hawaiian hawk present at area.
[B]Predators present, but no data from area.
[C]Pueo absent from or rare at area.
[D]Mongoose absent from area.

adverse effect on the pueo except perhaps when there is a crash in mice numbers, the main prey of both species.

The proportions of barn owl prey categories found in our study were similar to rodent and bird prey proportions from an analysis of 301 barn owl pellets from Hawai'i Island, O'ahu, and Kaho'olawe in a study by Snetsinger *et al.* (1994), but insects were considerably less common (frequency = 1%) in the latter. Other investigations have determined that barn owl pellets from Hawai'i Island were composed entirely of rodents (Tomich 1971: *n* = 100; Baker and Russell 1980: *n* = 31) although a study of barn owl stomachs from Kaua'i (Aye 1994) reported a high frequency of insects (present in 75% of 55 stomachs that contained food) and a relatively low frequency of rodents (48%). Similarly, we found insect prey to be common in pellets from Kaua'i (57%) as well as from Lana'i (57%).

In our study, bird prey in diets of the two owl species varied, with the pueo taking mostly introduced terrestrial passerine and non-passerine species and the barn owl a wider range of both endemic and introduced terrestrial passerine and non-passerine species (Table 1). However, in Hawai'i, the pueo and barn owl have been recorded preying not only on passerines but also on seabirds, and shorebirds (d'Arcy Northwood 1940; Byrd and Telfer 1980; Schulmeister 1980; Pyle 1987; Snetsinger *et al.* 1994; VanderWerf *et al.* 2007; Mounce 2008; Raine *et al.* 2017*a*, 2017*b*).

We note that despite the lack of statistically significant collection sizes, the data show that barn owls take more rats than pueo. Two factors could explain this. First, barn owls are larger than pueo, and rats may be difficult for the smaller owl to catch and handle. We assessed weights of owl study skins in the Bishop Museum. Barn owl study skins averaged 338 g (= 5), and pueo 260 g (*n* = 8). Rats weigh between 40 and 350 g (*R. norvegicus*, 125–350 g; *R. rattus*, 90–180 g; *R. exulans*, 40–80 g: Tomich 1986). Second, the two owls forage in different kinds of habitats and at different times of the day. Like rats, barn owls are nocturnal, but pueo are crepuscular. Barn owls forage in a wide variety of habitat types. Pueo forage primarily over open habitats like grasslands, pastures, and scrubland, habitats where rats are much less abundant than in mesic and wet forest.

Cat

The prey composition of cat scats in our study was broadly similar to that of pellets of the two owl species, although birds were more frequent. Similar frequencies of occurrence of rat, bird and arthropod prey in cat scats were reported from a Hawai'i Island study (Amarasekare 1994: *n* = 45) and the proportion of rodents in 87 Hawai'i Island cat scats examined by Snetsinger *et al.* (1994) were comparable to our Hakalau and Holei Pali values, but birds were more common (68%) and arthropods less common (17%) than in our collections. The cat, together with rats (Seto and Conant 1996; VanderWerf and Smith 2002; Nelson *et al.* 2002; Hess *et al.* 2007) are overall the most significant predators of native Hawaiian birds, including endangered species (Judge *et al.* 2012), although bird remains in cat scats in our study could not be identified. The cat is also a major threat to seabird breeding colonies (Smith *et al.* 2002; Lohr *et al.* 2013; VanderWerf and Young 2014).

Mongoose

In our study, food preferences of the mongoose differed from those of the two owl species and the cat, in that arthropods (small cockroaches in particular) were the predominant prey. Another study by Kami (1964) (*n* = 453) found that prey composition varied at three Hawai'i Island sites, with rodents present in 72% of scats at one site, although prey frequencies were generally comparable to ours. In their analysis of 86 scats from Hawai'i Island, Baldwin *et al.* (1952) also reported categories and proportions of prey similar to our findings. The mongoose's varied diet in Hawai'i (which includes frogs, toads, and crabs, in addition to the diverse prey categories we identified) has been reported by several workers (Muir 1913; Pemberton 1933; La Rivers 1948; Baldwin *et al.* 1952; Kami 1964; Amarasekare 1994). The mongoose and the cat in Hawai'i are targeted by predator control programs (e.g. VanderWerf and Young 2014). However, mongoose impacts on native species are not as significant as those of the cat (Hays and Conant (2007).

Prey choice and availability in the Hawaiian Islands

Both the barn owl and the pueo preyed more frequently on birds and insects than is reported in continental studies (see Mostello 1996 for review). This may be due in part to the depauperate nature of Hawai'i's small mammal fauna, which includes only one native terrestrial species (the Hawaiian hoary bat, *Lasiurus cinereus*) and five introduced species (one mouse, three rat, one mongoose species). The frequency of birds and insects as owl prey may also be related to the differences in foraging behaviour (see above). The diversity of birds that were barn owl prey may reflect its ability to take randomly encountered roosting birds, including native species if they are present. The pueo’s diurnal foraging behaviour and habitat (grasslands and pastures) would present opportunities to take many introduced birds (especially the zebra dove) as possible prey. Dickman (1996) found that invertebrates featured more prominently in diets of the cat from Pacific region islands ($n = 12$ studies) than from a range of habitats in mainland Australia ($n = 22$ studies). Additionally, non-mammalian prey may be elevated in diets of the two owl species due to relatively low population densities of the introduced small mammal species at some areas in the Hawaiian Islands (e.g. *R. rattus* on western Mauna Kea, Hawai‘i Island: Amarasekare 1994).

Small-scale variation in distribution and temporal availability and abundance of prey, as well as behavioural differences in foraging behaviour are sufficient to explain differences in diets among predators. Although there is considerable dietary overlap among these predators, competition among them seems unlikely due the opportunistic nature of their foraging behaviour and to the abundance of prey species. It is possible, however, that competition may become significant at times of food resource scarcity, as suggested by the reported cases of emaciation causing mortality in the two owl species.

Conflicts of interest

The authors declare no conflicts of interest.

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