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DO THE CONTENTS OF BARN OWL PELLETS ACCURATELY REPRESENT THE PROPORTION OF PREY SPECIES IN THE FIELD?[1]

YORAM YOM-TOV AND DAVID WOOL
Department of Zoology, Tel Aviv University, Tel Aviv 69978, Israel, e-mail: yomtov@ccsg.tau.ac.il

Abstract. Prey composition of Barn Owl *(Tyto alba)* pellets from northwestern Negev, Israel, was examined. The 414 individual specimens of mammals represented by 256 pellets comprised: 9.2% *Meriones sacramenti*, 41.1% *M. tristrami*, 8.2% *Gerbillus andersoni*, 40.1% *Mus musculus*, and 1.4% *Crocidura suaveolens*. The pellets also contained some remains of insects, small specimens of the snake *Eryx jaculus*, and two passerine birds. We tested whether the observed distribution of prey species in the 256 pellets could be obtained if owls hunted at random. Direct calculation and simulations indicate that more single-species pellets contained large mammals than would be expected from random sampling. In simulation of owls sampling at random from the database, the distribution of "pellets" containing 1, 2, 3, or more prey items was similar to the observed distribution only when a cumulative weight limit for pellet ejection was set at 80–100 g. Even when Barn Owls do not hunt some species preferentially, the contents of the pellets may be biased towards larger prey. This result should be taken into consideration when accumulated pellets are used in ecological and paleontological studies to approximate the distribution of mammal prey in real communities, present or past.

Key words: *Barn Owl,* Tyto alba, *pellets, prey selection.*

Do the contents of owl pellets represent the true proportions of the small mammal species in the community the owl preys upon? If the answer to this question is positive, these pellets may provide an important source of information for ecologists and paleontologists. This is so because determination of the present community structure is time-consuming and often inaccurate, and the ability to determine past community structure is remote (see review by Andrews 1990). The use of pellet contents as estimates of prey proportions in the field depends on two assumptions: first, that owls hunt at random, and second, that the pellets are a random sample of their catch. Both assumptions are difficult to test in the field.

It is often claimed that Barn Owls show no food preferences (Bunn et al. 1982) and that the numbers of each species represented in the diet are a true reflection of prey abundance (Hanney 1962, Glue 1971), or accessibility (Steyn 1983). However, this claim is based almost wholly on circumstantial evidence (Cramp 1985) and thus is controversial. Glue (1971) believed that the claim is apparently justified for assemblages of small rodents, and that the species representation in Barn Owl pellets is proportional to the relative abundance of the prey. Similarly, Mikkola (1983) concluded that the Barn Owl is a nonselective predator, whose diet reflects the abundance of small nocturnal mammal species within its hunting territory. However, Andrews (1990) suggested that " .. (Barn Owl's) prey reflects the particular needs and hunting behavior of the predator rather than being representative of any one habitat." In South Africa, Barn Owl prey determined from pellet analysis appears to have a different proportion of species than samples of the same prey species obtained by trapping (Perrin 1982), whereas the opposite was found in a similar comparison in Great Britain (Glue 1967). Prey size is an obvious limiting factor in comparing pellet analyses with data from field trapping (Andrews 1990), as large prey species are taken in greater numbers during the breeding season than at other times of the year (Buckley and Goldsmith 1972). Nevertheless, within the size limits of prey taken by the Barn Owl, the size distribution of prey in the diet could be similar to the size distribution of the mammal community from which the diet is derived.

The fact that there is no general agreement that owls sample their prey randomly is partly due to the absence of knowledge about the abundance of their prey. Prey abundance is often studied by trapping, but this method is often biased because prey species react differently to traps: some are attracted to them, whereas others may be trap-shy (Blem et al. 1993). For example, two of the eight species of rodents occurring in the sand dunes of the western Negev in Israel avoid most types of traps (Yom-Tov 1991). In the absence of information on the hunting behavior of owls, we concentrate on the second assumption: using a collection of Barn Owl pellets from the northwestern Negev, Israel, we test in computer simulations whether the distribution of prey species in pellets could be obtained by randomly sampling a "field" containing the prey in the proportions observed in the total catch.

METHODS

STUDY SPECIES

The Barn Owl is nearly cosmopolitan and its food habits have been studied extensively. Rodents are its most

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frequent prey everywhere, with microtines the most common prey in Europe, replaced by gerbils in drier regions of the Old World. The daily food intake of the Barn Owl in Europe is 70–104 g live prey weight (Mikkola 1983), and in South Africa 42–82 g (Steyn 1983). An average of 1.4 pellets are produced daily (Schmidt 1977). Because Barn Owls have strong fidelity to roosting places, and use the same roosts year after year, large accumulations of pellets may build up. Adult Barn Owls swallow most of their prey whole, but large prey may be dismembered. The skulls of small mammal prey are rarely intact, because such prey are commonly killed by breaking the neck and the back of the skull. However, 75% of small rodent skulls in Barn Owl pellets have at least intact maxillary and frontal bones and about 80% of mandibles are complete. Similarly, almost all major skeletal elements (for example, 98% of tibiae) found in Barn Owl pellets are complete (Andrews 1990), facilitating prey identification.

STUDY AREA AND MATERIAL

Pellets of Barn Owls were collected along a road near Kibbutz Magen, western Negev, Israel (31°17′N, 34°24′E). This is a semi-desert, sandy-loess plateau, where annual rainfall is about 300 mm. The road is lined with *Tamarisk* and *Eucalyptus* trees which are used as roosts by the owls. Several species of owls are known from this area, but by far the most common is the Barn Owl, whose pellets are easily distinguished from other co-occurring owls (the much smaller Little Owl [*Athene noctua*], the much larger Eagle Owl [*Bubo bubo*] and the rare wintering Short-eared Owl [*Asio flammeus*] and Long-eared Owl [*Asio otus*]). Average dimensions of pellets of Barn Owl, Little Owl, and Eagle Owl are 50 × 27 × 22 mm, 25 × 14 × 14 mm, and 77 × 30 × 27 mm, respectively (Mikkola 1983). On 9 May 1996, all pellets along a stretch of about 1.5 km of the road were collected by a group of experienced rangers of the Nature Reserve Authority of Israel. Each group of 2–4 rangers searched the ground area of about 100 × 10 m for about one hour, collecting all pellets found. Because Barn Owl pellets are compact and decompose slowly (Mikkola 1983) and mean annual rainfall in the area is low, it is likely that the pellets were accumulated there during at least a year. In our study area, all the rodent and mammalian insectivore species are nocturnal, thus they all are potential prey for the nocturnal owls.

Pellets (n = 256) were brought to the laboratory, soaked in water for several hours and the bones separated. Pellets were examined individually. Prey species were identified under a stereomicroscope by comparison with the large collection of local mammals in the Zoological Museum of Tel Aviv University. The number of prey items in each pellet was determined by counting the number of the most common identifiable bones in the pellet (for example, the number of left or right mandibles or tibiae). The main bones used for species identification were the mandibles, the cranium (whole or broken) and the tibia. When possible, the following measurements were taken: the length of the tibia, total length of the mandible, total length of the lower molar row, total length of the upper molar row, the length of the diastema, the greatest length of the skull and three measures of skull breadth: across the zygomatic arches, across the tympanic bullae, and between the orbits.

DATA ANALYSIS

The pellets contained the remains of five species of mammals which differed greatly in size (see Results). If the owls had caught their prey at random, irrespective of species and size, then the proportions of the five species among all individual prey items recovered from the pellets represent their proportions in the hunting area of the owls. We do not know whether this is true, but we used these proportions as the database to test the assumption that the pellets are a random sample from the total catch of the owls. Three approaches were taken to test this assumption.

(1) Direct calculations. If the above assumption is true, then the proportions of the five species in pellets containing only one animal (total of 162 pellets), should be the same as in the database. For pellets containing the remains of two animals (60 pellets), the expected proportions of each combination of the five species is given by the expansion of the polynomial $(a + b + c + d + e)^2$, where the letters a–e represent the proportions of the five species in the database. We tested this assumption for pellets containing one or two prey items per pellet. There were too few pellets with more than two animals, and too many possible combinations of the five mammalian species, for the direct calculations of the expected catches to be useful. We therefore resorted to simulations.

(2) Simulation 1. There are 15 possible combinations of pairs of species from the database. A Resampling Stats (Simon 1995) routine was modified for the analysis. Instead of species codes, their weights were used as data. The program sampled (with replacement) two individuals from the database at random and printed their combined weight. The differences in weight between species were so large that when two items were sampled and summed, their sum clearly identified the sampled pair of species. The frequency of occurrence of each pair of species in many runs of the program was recorded as their expected frequency.

(3) Simulation 2. If the owls show no preference for a species and hunt at random, but are affected by some limit of prey weight (LIM) in deciding whether or not to eject a pellet, how many pellets would be expected to contain 1, 2 or more animals? To simulate this situation, the Resampling Stats program package was used again. A sequential sampling routine was written such that the owl would select its first prey item at random from the database. If that item is equal to or heavier than LIM, then a pellet is produced and the cycle repeated. If the first prey is smaller than LIM, then another prey item is caught and the weight added until LIM is reached. The program records the number of cases of 1, 2, 3, etc. prey per pellet, given a fixed LIM. If the observed frequencies agree with expectation, then LIM may be the critical weight level causing departure of observed frequencies of numbers of mammals per pellet from random expectations. Seventeen simulation runs were made, 100 to 300 pellets simulated each time, with LIM set at values between 70

TABLE 1. Observed frequencies of five mammal species in owl pellets, and the expected frequencies, calculated from model field probabilities, in pellets containing a single prey item (*C. suaveolens* was not present in the single-species pellets, and was omitted from the calculation of χ^2).

Species	Observed	Expected
Meriones sacramenti	29	14.9
Meriones tristrami	111	66.6
Gerbillus andersoni	4	13.3
Mus musculus	18	65.0
Crocidura suaveolens	0	2.2
Total	162	162

and 200 g. The final run with LIM = 150 g simulated 1,000 pellets.

RESULTS

PELLET CONTENTS

The sample included 256 pellets and contained 414 small mammals belonging to five species. The pellets also contained some remains of insects, two small specimens of the snake *Eryx jaculus* and two unidentified passerine birds. The 414 individual mammal specimens comprised: 9.2% *Meriones sacramenti* (MS), 41.1% *M. tristrami* (MT), 8.2% *Gerbillus andersoni* (GA), 40.1% *Mus musculus* (MM), and 1.4% *Crocidura suaveolens* (CS). We used these proportions as the database. These five species differ greatly in size and their average adult body masses are 120, 70, 25, 15, and 7 g for MS, MT, GA, MM, and CS, respectively (Mendelssohn and Yom-Tov 1987). Three other potential prey species which are known to occur in the study area were not found in the pellets: the Long-eared hedgehog *Hemiechinus auritus* and the East European hedgehog *Erinaceus concolor* are probably too large for the Barn Owl (their respective mean body masses are 200 and 600 g), and the Jerboa (*Jaculus jaculus*) is not common in the study area.

The main identifiable bones found in the pellets were mandibles, broken maxillae and tibiae. Among the smaller species (GA, MM, and CS) there were no complete skulls, but among the larger MT there were 34 (25.5%) complete or almost complete skulls, and among the largest species in the sample (MS, 120 g), there were 19 complete skulls (73.1%). This was probably due to the fact that larger skulls are thicker than small ones, and able to withstand better the pressure applied to them by the muscles of the proventriculus of the predator.

For most of the measured skull characters, the size range and variance of the prey found in the pellets was larger than that reported for adult specimens of the same species by Mendelssohn and Yom-Tov (1987) although the means were similar. This is true for most variables for which we have data.

DIRECT CALCULATIONS

One animal per pellet. Most pellets (62.5%) contained only a single prey item, whereas the rest contained 25 different combinations of the various prey species, with one pellet containing remains of four species and another pellet with remains of eight prey from four species. The observed frequencies of the five species in pellets containing a single prey item, and the frequencies expected from random sampling in the database, are presented in Table 1. There was a significant deviation from expectation ($\chi^2_3 = 85.6$, $P < 0.001$): the pellets contained many more large prey items (MS and MT) than expected from random sampling in the database.

Two prey items per pellet. The expected frequencies for the 15 possible paired combinations of five species were calculated from the polynomial expansion; similar expected numbers also were obtained from 600 runs of the simulation program. Because there were only 60 two-animal pellets observed, the expected numbers in some combinations were too small to be tested. Pooling small groups together for the χ^2 analysis (Sokal and Rohlf 1995), the observed frequencies were not significantly different from random expectation ($\chi^2_4 = 7.8$, $P > 0.05$, data not shown). It should be noted that only a few of the large mammal species were present in pellets with two animals, and the observed frequencies are therefore biased towards smaller size. When we grouped the 60 observed pellets into those containing two small prey (combined weight less than 50 g), intermediate (51–105 g) and large (> 106 g) mammal species (Table 2), significantly more pellets contained two small or intermediate sized mammals, and significantly fewer contained large individuals (actually no pellet contained two MS individuals) than expected by random sampling of two individuals from the database ($\chi^2_2 = 6.7$, $P < 0.05$). This raises the suspicion that prey weight (or size) does affect the contents of the pellet.

SIMULATIONS

Numbers of prey items per pellet, constrained by prey weight. Sequential sampling from the database produced distributions strongly dependent on LIM, the fixed weight. None of the expected distributions was identical to the observed distribution. When LIM was smaller than 90 g, the distribution was similar to but more J-shaped than the observed (more pellets are expected to contain a single individual than observed). When LIM is increased to 100 g or more (120 and 200 g are listed in Fig. 1), the distribution has a clear mode at two individuals per pellet, very unlike the observed distribution. Intermediate values of LIM between 90 and 100 g did not improve the fit to the observed distribution. Interestingly, when the pellets were classified

TABLE 2. Observed and expected frequencies of pairs of mammals in 60 pellets when classified into three weight classes for tests of significance.

Class	Observed	Expected
Small (< 50 g)	19	13.7
Intermediate (51–105 g)	28	23.9
Large (> 105 g)	13	22.4
Total	60	60.0

by the approximate weights of the animals they contained (based on weight data of adults in Mendelssohn and Yom-Tov 1987), the resulting distribution had a mode of 80–100 g (Fig. 2).

DISCUSSION

The relatively wide range of size and the large variance of the individual prey may indicate that the pellets contained not only adults but also young prey, as is generally true for owls (Mikkola 1983). Our results indicate that more large mammals are included in single-species pellets than is expected from random sampling, with or without a weight limit. This could be because the owls prefer large prey, or because it is necessary to eject a pellet of a large animal remains before new food can be ingested (Duke et al. 1976).

For a predator, particularly an owl hunting from an observation point, there may be an advantage to hunting large prey, as the return for the energy expended on each hunting flight is greater. However, for any predator, and particularly a flying one, there may be an upper limit for prey size which can be captured and carried away. The results of our simulation suggest that optimal prey weight for Barn Owls may be between 80–100 g, a value that is less than the weight of adult *Meriones sacramenti*, the heaviest prey animal (120 g) in our sample of pellets. This might be explained by the fact that when eating large prey, Barn Owls tend not to swallow it whole, but to tear it into smaller pieces (Yom-Tov, pers. observ. of captive birds).

There were 29 pellets with one MS, four pellets contained both MS and MT (190 g), one pellet contained MS with MM (135 g), two pellets contained MS with three MM (165 g), and one pellet contained MS with seven MM (225 g). One pellet contained a combination of species with MS whose total fresh weight was 240 g. No pellet contained more than one MS. If LIM is lower than 100 g, the simulation results depend on which animal is captured first. If the initial prey is as large or larger than LIM (i.e., if the first animal is MS or MT), only one animal will be contained in the pellet. MT was much more abundant in the database than MS, and it was likely that MT was most often sampled first (the other very common species, MM is small, and if caught first, would cause the program to continue and "catch" another prey). If LIM is more than 100 g, the first animal captured (either MT or MM are the most likely) will not suffice to keep the owl from seeking more prey, and two or more animals will be included in the resulting pellet. We do not know if owls do in fact make feeding decisions on the same principle as the simulation program, but it would make biological sense if they did.

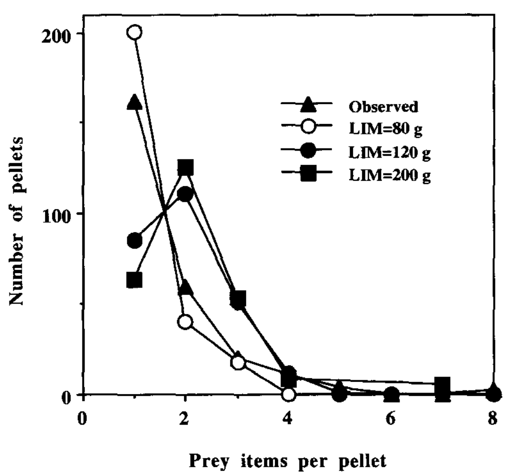

FIGURE 1. Comparison of observed and simulated distributions of the numbers of prey items per pellet. Note that LIM = 80 g fits the observed distribution.

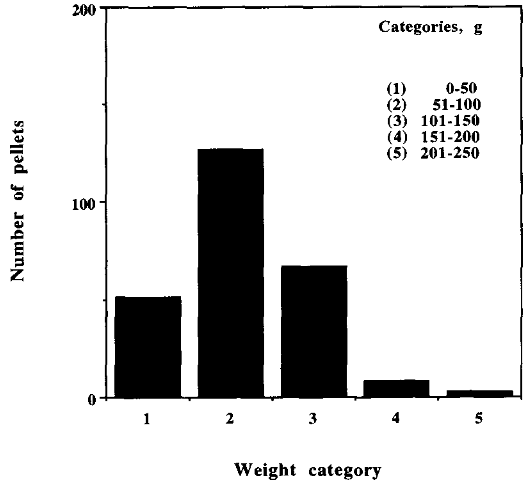

FIGURE 2. Distribution of estimated body mass of mammals from 256 Barn Owl pellets, assuming all remains belonged to adult prey. Weights from Mendelssohn and Yom-Tov (1987).

In conclusion, the contents of Barn Owl pellets do not truly represent the proportions of prey species in the database. Even if Barn Owls do hunt at random, the contents of the pellets may still be biased towards the larger prey if the potential prey differ in size. This result should be taken into consideration when accumulated pellets are used in ecological and paleontological studies to approximate the distribution of mammal prey in real communities, present or past.

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TERRITORIAL RESPONSES OF BOREAL FOREST BIRDS TO HABITAT GAPS[1]

JEAN-FRANÇOIS RAIL[2]
Centre d'Études Nordiques et Département de Biologie, Université Laval, Ste-Foy, Québec, G1K 7P4, Canada

MARCEL DARVEAU AND ANDRÉ DESROCHERS
Centre de Recherche en Biologie Forestière et Département des Sciences du Bois et de la Forêt, Université Laval, Ste-Foy, Québec, G1K 7P4, Canada

JEAN HUOT
Centre d'Études Nordiques et Département de Biologie, Université Laval, Ste-Foy, Québec, G1K 7P4, Canada

Abstract. We used playback trials to determine whether birds will cross treeless gaps to respond to simulated territorial intruders. We evaluated the effect of gap width on responses by five forest bird species. We found that for forest specialists such as the Swainson's Thrush (*Catharus ustulatus*), Golden-crowned Kinglet (*Regulus satrapa*), and the Black-throated Green Warbler (*Dendroica virens*), the probability of crossing gaps decreased sharply with gaps 25–40 m wide. By contrast, control trials showed no significant decrease in their probability of response up to 100 m through continuous stands. Habitat generalists such as the White-throated Sparrow (*Zonotrichia albicollis*) and the Dark-eyed Junco (*Junco hyemalis*) were more prone to cross treeless gaps than forest specialists. Playback studies provide a new tool for understanding birds' responses to microscale habitat discontinuities.

Key words: boreal, breeding birds, forests, forest gaps, logging, Québec, territorial response.

In forest-dominated landscapes, forestry roads, water bodies, and small scale clearcuts are often abundant. Should we consider forests featuring these relatively narrow gaps as continuous breeding habitat for birds? Small-scale forest fragmentation may not alter population processes like dispersal and recolonization by birds, but few studies address its impact on avian activities such as territorial defense. Songbirds may exhibit variation in their behavioral response to habitat gaps depending upon gap width and species involved. For example, it is likely that < 5-m wide gaps in the

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[2] Present address: Canadian Wildlife Service-Québec Region, P.O. Box 10 100, Ste-Foy, Québec, G1V 4H5, Canada, e-mail: jean-francois.rail@ec.gc.ca