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Planning for success: Serengeti lions seek prey accessibility rather than abundance

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Summary

1. We used long-term radio-telemetry data to investigate how Serengeti lions (*Panthera leo*) distribute themselves with respect to hunting opportunities. Specifically, we investigate whether lions hunt in areas where prey are easy to capture or where prey are locally abundant.

2. We used resource-selection functions (logistic regressions) to measure the location of kills/carcasses with respect to five different habitats: the view-sheds from large rocky outcrops, river confluences, woodland vegetation, erosion embankments and water sources.

3. As expected for a sit-and-wait predator, resting lions spent more time in areas with good cover. On a broad-scale, lions shifted their ranges according to the seasonal movement of prey, but at a finer scale (< 100 m) lions fed in areas with high prey 'catchability' rather than high prey density. Plains lions selected erosion embankments, view-sheds from rocky outcrops, and access to free water. Woodland lions tended to use erosion embankments, and woody vegetation.

4. The results emphasize the importance of fine-scale landscape and habitat features when assessing predator–prey theory and conservation.

Key-words: ambush predator, habitat selection, predator-sensitive foraging, predator–prey interaction, prey abundance, resource selection.

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Introduction

Studies of risk-sensitive foraging rarely focus on the behaviour of the predator (Lima 2002), and furthermore the role of landscape in influencing the catchability of prey is often overlooked when examining predator–prey interactions. While most animals seek landscape features with adequate food, shelter, nest sites or other resources (Manly *et al*. 2002), the choice of feeding habitat for a sit-and-wait predator is less clear. One possibility is simply to hunt where prey are most abundant (as described for numerous carnivores: Litvaitis, Sherburne & Bissonette 1986; Murray, Boutin & O'Donoghue 1994; Thom *et al*. 1998; Pike *et al*. 1999; Palomares *et al*. 2001; Spong 2002). However, ambush predators might often benefit by hunting in areas where prey are locally scarce. Habitats with good cover and camouflage may be so dangerous that prey tend to avoid them, preferring to feed in more open habitats (Pienaar 1974; Sinclair 1985; Prins & Iason 1989; FitzGibbon & Lazarus 1995; Sinclair & Arcese 1995; Bouskila 2001). Nevertheless, prey may occasionally be forced to utilize high-risk habitats in order to obtain essential resources and consequently suffer higher predation (Hik 1995). Lions (*Panthera leo*) are opportunist stalk-and-ambush hunters, relying on a combination of good cover, acceleration, body weight and occasional cooperation with other pride members to overcome their prey (Schaller 1972; Elliott, Cowan & Holling 1977; van Orsdol 1984; Packer, Scheel & Pusey 1990; Scheel & Packer 1991; Stander 1992; Scheel 1993; Stander & Albon 1993; Packer & Pusey 1997). Using 16 years of data on radio-collared lions, we test the relative importance of habitat features (referred to as the ambush-habitat hypothesis) vs. local prey density (the prey-abundance hypothesis) in the Serengeti ecosystem, Tanzania. Under the ambush-habitat hypothesis, the lions should spend more time and make more kills than expected in habitats with greater cover, whereas the prey-abundance hypothesis predicts that the lions should prefer areas where their primary prey are at the highest densities (Pennycuick 1975; Maddock 1979). Grass length provides an important indicator of prey density

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in our study because open swards of short-grass are maintained primarily by large herds of grazing ungulates (McNaughton 1983).

Lions obtain a significant proportion of food by scavenging, and we predict that these feeding sites will be associated with different habitat features than kills. Because lions scavenge on ungulates that have died from starvation, disease or predation by cursorial species such as hyenas and cheetah (Kruuk & Turner 1967), scavenged carcasses should be located more often in areas of high prey abundance rather than favourable ambush features (Sinclair 1979; Sinclair & Arcese 1995).

Habitat selection by carnivores has been investigated by various authors (Litvaitis *et al*. 1986; Crawshaw & Quigley 1991; Murray *et al*. 1994; Kurki *et al*. 1998; Meyer, Irwin & Boyce 1998; Thom *et al*. 1998; Gros & Rejmanek 1999; Pike *et al*. 1999; Funston, Mills & Biggs 2001; Glenz *et al*. 2001; Palomares *et al*. 2001; Edwards *et al*. 2002). Resources are 'selected' when they are used disproportionately more often than their availability (Manly *et al*. 2002). We tested for selection of specific habitats using goodness-of-fit exact tests and logistic regression resource-selection functions (which permits multiple candidate factors to be combined into a single predictive equation, Boyce & McDonald 1999; Manly *et al*. 2002). All analyses are separated according to season because the prey's willingness to enter risky habitats is highest when resources are scarcest (McNamara & Houston 1987; Lima & Dill 1990; Ludwig & Rowe 1990; Clark 1994; Hugie & Dill 1994; Sinclair & Arcese 1995).

Materials and methods

THE STUDY AREA

The study was conducted in a 1800 km^2 area in the south-eastern portion of the Serengeti National Park Tanzania between 2°22′ and 2°55′ South and 34°45′ and 35°14 East. The study area is characterized by *Acacia* and *Commiphora* woodlands in the northern third, treeless long-grass plains in the centre and treeless short-grass plains in the south. Each study pride is classified as residing primarily in the woodlands or the plains.

Average annual rainfall of 700 mm falls primarily during the wet season (November–May). The dry season occurs from June to October. Large herds of wildebeest *Connochaetes taurinus* (~1·2 million), zebra *Equus burchelli* (~200 000) and gazelles *Gazella thomsoni* (~250 000) migrate onto the short-grass plains during the wet season where they give birth and feed on calcium-rich grasses. The migratory herds pass through the northern (woodland) part of the study area during the beginning and end of each dry season.

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GEOGRAPHIC INFORMATION SYSTEM (GIS) ANALYSIS

Land contours, kopjes (rocky inselbergs) and rivers were extracted from 1 : 50 000 topographic maps of the Serengeti National Park using ArcView 3·2 with the Spatial Analyst and 3D Analyst extensions (projection: UTM, units: metres, datum: ARC 1960, spheroid: Clarke 1880).

CARCASS DENSITY IN MAJOR HABITATS

The extent of the three major habitats (woodlands, long-grass and short-grass plains) was estimated by sampling a 2 × 2 km grid. The number of kills and scavenges in each area was calculated separately for dry and wet season and compared with an expected value (based on area) using a χ^2 test. The data were corrected for search bias as the short-grass plains were searched less frequently than long-grass areas. The expected number of kills was adjusted according to the total number of observations made in each area. Data were restricted to radio-collared lions to minimize search bias from differences in visibility.

DATA COLLECTION AND SAMPLING DESIGN

Between 1984 and 2000, radio-collared lions were located weekly from a vehicle on 10,151 occasions using VHF radio collars (telemetry data are unbiased with respect to habitat type). For the feeding analysis of radio-collared lions, we included only carcasses that could reliably be classified as a kill ($n = 203$) or as a case of scavenging ($n = 66$).

Habitat was measured on a 2 × 2 km grid throughout the study area with additional data on riparian habitats recorded every 3 km along major drainage lines. Each point on the systematic grid, drainage and lion feeding sites were classified by the following habitat features: (1) the area in view by a lion while on top of a kopje (the 'view-shed'), (2) river confluence, (3) erosion embankment, (4) woody vegetation and (5) proximity to water.

The view-shed is calculated in ArcView 3·2 using the height of the kopje and a digital elevation model (triangular irregular network) of the surrounding area. We estimated the maximum distance that could be viewed from plains kopjes to be 3·5 km vs. 1·5 km for woodland kopjes (due to low visibility in thick vegetation). Each grid coordinate was identified as being located inside or outside a view-shed. Confluences were defined as areas within a 500 m radius of the junction between two drainages. Plains drainages are typically shallower with less woody vegetation than woodland drainages (Gereta & Wolanski 1998), so we included only confluences of plains-drainage lines that were > 3 km long vs. woodland-drainage lines > 2 km. Each point was either inside or outside a 500 m radius from a confluence. Erosion embankments were defined as being greater than 0·4 m high (based on minimum cover requirements for lions: Elliott *et al*. 1977; van Orsdol 1984; Scheel 1993). Such embankments could be formed from river banks, erosion terraces from eroded game trails as well as road ditches. We scored the total length (m) of erosion bank within 100 m of each point. The percentage of woody vegetation greater than 0·4 m high was averaged from four equidistant measurements at a radius 15 m away from a given point.

Ephemeral pools are mainly available in the wet season (Gereta & Wolanski 1998), and we recorded (a) the cumulative monthly rainfall between September 1999 and August 2000 at 15 locations around the study area and (b) the pools closest to the headwaters of each drainage (water was assumed to be largely available downstream of each top-most pool). These data were used only to estimate the spatial distribution of water during the dry season (defined as months with less than 50 mm of precipitation). For the wet season, we assumed that water was available all along every drainage line. The proximity (to the nearest 10 m) of each survey/carcass point to the closest available free water was calculated using the Nearest Feature extension in ArcView 3·2 and transformed so that the closest distances were most positive.

STATISTICAL ANALYSES

We investigated the habitat-utilization of all radio-collared lions from 1984 to 2000 using traditional χ^2 goodness-of-fit tests, and the observed numbers of kills and scavenges in relation to these landscape features using goodness of fit exact tests (χ^2_E). The goodness of fit exact tests are outlined in Appendix I and adjusted for multiple comparisons using the Bonferroni correction ($\alpha = 0{\cdot}05/5 = 0{\cdot}01$). For all the univariate statistics, the habitat features were broken into the following categories: observations were either (i) in or out of a view-shed, (ii) in or out of a confluence, (iii) at distances of 0 m, 1–75 m, 76–125 m, 126–175 m, 176–250 m, 251 + m from erosion embankments, (iv) within 15 m of 0–5%, 6–10%, 11–20%, 22–35%, 36–100% woody vegetation, and (v) at distances < 50 m or > 50 m from free water.

Binary logistic regressions predicting kill vs. non-kill (or scavenged carcass vs. non-carcass) were calculated in SPSS 11·0. The logistic regressions used the stepwise backward-elimination process based on the Wald statistic. Variables were considered to be significantly different from zero if the *P*-value was less than 0·2, as opposed to the usual 0·05. Because of colinearity between independent variables, the 0·2 significance level prevents potentially important variables from being dropped from the multivariate analysis (Tabachnick & Fidell 1996). The odds ratio [e^{β} where $\beta_{1\ldots P}$ are the coefficients for each habitat (1 … *P*)] was determined for each habitat variable. If the odds ratio is greater than 1, β is positive, suggesting an increased occurrence of a kill or scavenged carcass (Tabachnick & Fidell 1996).

We tested for non-linear relationships in the logistic models by including squared functions. If continuous variables behave quadratically, we would expect the coefficients from the logistic regression to be negative. For instance, if β for vegetation is positive and β for $(\text{vegetation})^2$ is negative, this implies that excess vegetation hampers hunting success, and thus the relationship between hunting success and vegetation is non-linear.

Results

The major prey species for plains lions were wildebeest *Connochaetes taurinus*, zebra *Equus burchelli*, Thomson's gazelle *Gazella thomsoni* and warthog *Phacochoerus aethiopicus*; the woodland lions also killed buffalo *Syncerus caffer*. Incidental species included eland *Taurotragus oryx*, Grant's gazelle *G. granti*, kongoni *Alcelaphus buselaphus*, reedbuck *Redunca redunca* and topi *Damaliscus korrigum*.

The distribution of radio-collared lions from 1984 to 2000 (*n* = 10 151) indicates that lions spend more time than expected in areas with good cover, regardless of season (Table 1 and Fig. 1).

CARCASS DENSITY IN MAJOR HABITATS

Although the distribution of kills shifted toward the short-grass plains coincident with the wet season migration (Fig. 2), there were fewer kills on short grass than expected on the basis of available area (wet season kills $\chi^2_{\text{corrected}} = 18{\cdot}29$, $P < 0{\cdot}001$). In contrast, carcasses scavenged during the wet season were found in direct proportion to the availability of short grass ($\chi^2_{\text{corrected}} = 0{\cdot}74$, $P > 0{\cdot}3$.

FINE-SCALE HABITAT CHARACTERISTICS FOR FORAGING (UNIVARIATE RESOURCE SELECTION)

More kills than expected occurred in eroded areas as well as in areas with thicker vegetation, river confluences and drainages containing free water (Tables 2 and 3).

Table 1. Resource-selection results from χ^2 tests for all observations of radio-collared lions from the plains and woodlands. Signs indicate if lions were observed more (+) or less (–) often than expected ($P \le 0{\cdot}1$). ***$P < 0{\cdot}001$, **$P < 0{\cdot}01$, *$P < 0{\cdot}05$

			All observations of radio-collared lions			
	Predictions		Plains		Woodlands	
Habitat features	Prey (H_{A1})	Habitat (H_{A2})	Dry (*n* = 2044)	Wet (*n* = 2496)	Dry (*n* = 2637)	Wet (*n* = 2974)
Erosion	–	+	+***	+***	+***	+***
Vegetation	–	+	+***	+***	+***	+***
View-shed	–	+	+***	+***	+*	+***
Confluence	–	+	+***	+***	+***	+***
Water	–	+	+***	+***	+***	+***

Fig. 1. The distribution of all radio-collared lion observations on the plains from 1984 to 2000 during (a) the dry season and (b) the wet season.

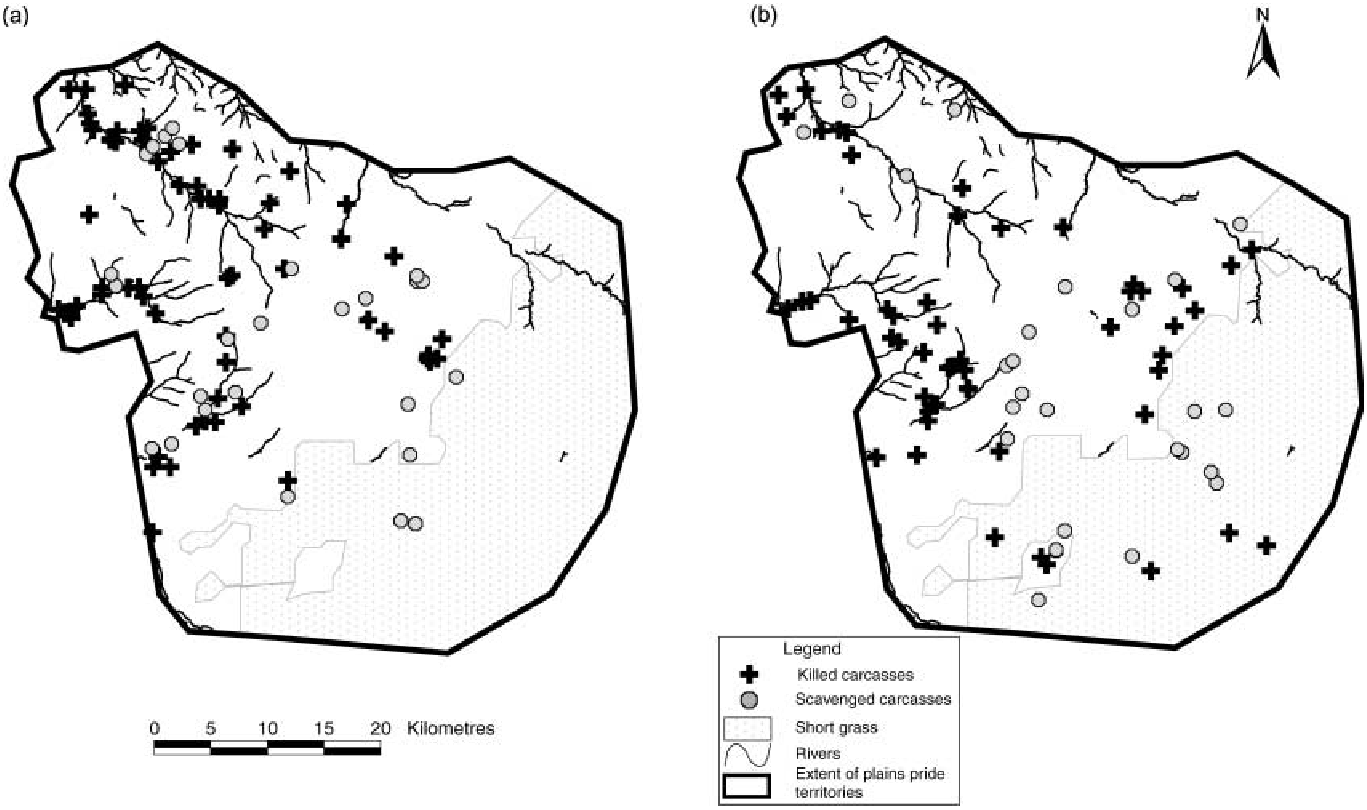

Fig. 2. The short-grass plains in relation to the distribution of kills and carcasses obtained by scavenging by plains lions during (a) the dry season and (b) the wet season.

Table 2. Resource-selection results from goodness-of-fit exact tests for plains and woodland lion kills. Signs indicate if kills occurred more (+) or less (–) often than expected, and signs in brackets are marginally significant ($P \le 0{\cdot}1$). ***$P < 0{\cdot}001$, **$P < 0{\cdot}01$, *$P < 0{\cdot}05$

			Kills			
	Predictions		Plains		Woodlands	
Habitat features	Prey (H_{A1})	Habitat (H_{A2})	Dry ($n = 64$)	Wet ($n = 56$)	Dry ($n = 63$)	Wet ($n = 20$)
Erosion	–	+	+***	+***	+***	+**
Vegetation	–	+	+*	NS	+***	+***
View-shed	–	+	NS	(+)	–**	NS
Confluence	–	+	+**	+**	+***	NS
Water	–	+	+***	+***	+***	NS

Table 3. Resource-selection results from goodness-of-fit exact tests for plains and woodland lion scavenged carcasses. Signs and significance levels are the same as in Table 2
Scavenged carcasses

			Scavenged carcasses			
	Predictions		Plains		Woodlands	
Habitat features	Prey (H_{A1})	Habitat (H_{A2})	Dry ($n = 26$)	Wet ($n = 26$)	Dry ($n = 10$)	Wet ($n = 4$)
Erosion	–	+	NS	+**	NS	NS
Vegetation	–	+	NS	NS	–***	NS
View-shed	–	+	(+)	+*	NS	NS
Confluence	–	+	NS	NS	NS	NS
Water	–	+	NS	NS	NS	NS

Table 4. Results of logistic regression analyses summarizing the significant habitat features for the location of kills. Signs indicate that the probability of a kill increases (+) or decreases (–) with cover (or proximity to water). Results in brackets indicate non-significant trend ($P < 0{\cdot}20$); ***$P < 0{\cdot}001$, **$P < 0{\cdot}01$ and *$P < 0{\cdot}05$. †Indicates result that was significant only in the multivariate tests; all other results were significant in both univariate and multivariate analyses

			Kills			
	Predictions		Plains		Woodlands	
Habitat features	Prey (H_{A1})	Habitat (H_{A2})	Dry ($n = 64$)	Wet ($n = 56$)	Dry ($n = 63$)	Wet ($n = 20$)
Erosion	–	+	+***	+***	+***	+
Vegetation	–	+	NS	NS	+***	+**
$(\text{Veg})^2$			NS	NS	NS	NS
View-shed	–	+	NS	+	NS	+†
Confluence	–	+	NS	NS	NS	NS
Water	–	+	+***	+*	NS	NS

View-sheds on the plains contained more scavenged carcasses than expected but not more kills. In the woodlands, view-sheds were not associated with either kills or scavenged carcasses. In general, the univariate analysis of carcass distributions indicated that more landscape features were selected for hunting (four features) than for scavenging (one feature).

PREDICTING LION FORAGING (RESOURCE-SELECTION FUNCTIONS)

The logistic-regression models that best predicted the location of kills and scavenged carcasses included vegetation as a quadratic, but not $(\text{erosion})^2$ or $(\text{distance to water})^2$. Thus, there was an indication of a non-linear relationship with vegetation. In contrast, the chance of a kill or scavenged carcass increased linearly with proximity to water and the degree of terracing. Consistent with the univariate analyses, most of the significant landscape features were positive (Tables 4 and 5).

Plains kills

Erosion embankments and proximity to water both contributed to the logistic-regression equation during the dry season (Table 4). The wet season regression included erosion embankments, proximity to water and view-sheds from kopjes (Table 4).

Table 5. Results of the logistic regression analyses summarizing the location of scavenged carcasses. Signs and significance levels defined in legend to Table 4

			Scavenged carcasses			
	Predictions		Plains		Woodlands	
Habitat features	Prey (H_{A1})	Habitat (H_{A2})	Dry (*n* = 26)	Wet (*n* = 26)	Dry (*n* = 10)	Wet (*n* = 4)
Erosion	–	0	NS	+*	NS	
Vegetation	–	0	NS	NS	NS	
(Veg)^2			NS	NS	NS	
View-shed	–	+	+	+*	NS	
Confluence	–	0	NS	NS	NS	
Water	–	0	(+)	–**	NS	

Woodland kills

The dry season regression model included both erosion embankments and woody vegetation (Table 4). The wet season model included erosion embankments, woody vegetation and view-sheds (Table 4).

Plains scavenged carcasses

The dry season logistic regression included the view-shed from kopjes and proximity to water (Table 5); the wet season model included view-sheds, proximity to water and erosion terraces (Table 5).

Woodland scavenged carcasses

None of the habitat features predicted the distribution of scavenged carcasses by woodland lions during the dry season. Too few carcasses (*n* = 4) were scavenged in the wet season to analyse effectively.

Discussion

The most important finding from this study was that although the landscape features used by plains and woodland lions differ, on a fine scale (< 100 m) lions select areas where prey are easier to catch, rather than areas where prey densities are highest. Prey tend to avoid dangerous areas with dense cover (Sinclair 1985; Prins & Iason 1989; FitzGibbon & Lazarus 1995; Sinclair & Arcese 1995). The grasses of the Serengeti plains are kept short by the high utilization of large herds of grazing ungulates (McNaughton 1983). However, lions spend less time (Table 1) and make fewer kills than expected on the short-grass areas, counter to predictions of the prey-abundance hypothesis. In contrast, the ambush-habitat hypothesis was supported by the univariate goodness-of-fit tests (Tables 2 and 3) and the logistic regressions (Tables 4 and 5), which generally indicate a positive relationship between greater cover and (a) lion habitat preferences and (b) more frequent lion kills. Taken together, these results suggest that lions select fine-scale areas where prey are easier to catch.

Erosion embankments and proximity to water were important features for hunting on the plains. View-sheds were useful in the wet season only when prey densities were highest. Lions did not select woody vegetation on the plains probably because there were so few trees in that broad-scale habitat. Woodland lions made more kills near erosion embankments, woody vegetation and perhaps water (Table 2). However, water was not significant in the logistic regression probably because of colinearity with erosion (river banks) and (riverine) vegetation.

Erosion embankments are often associated with riverbanks and eroded animal paths, and provide lions with cover while stalking prey. Access to water provides predictable locations for encountering prey, but vegetation at waterholes is equally important. Because lions were found more often in these same areas even in the absence of a carcass (Table 1), they may be selected for other reasons besides hunting (e.g. shade, safe denning sites).

The location of scavenged carcasses was associated with view-sheds from kopjes by plains lions, probably because of their broad vantage point. The views from woodland kopjes may be too obscured by vegetation to be useful for scavenging. Erosion embankments increased the probability of finding scavenged carcasses during the wet season, hinting that other plains predators may also hunt along erosion embankments. None of the habitat features were significant in predicting the location of scavenged carcasses for the woodland lions, implying that these carcasses may occur at random across this broad-scale habitat.

There is compelling evidence that herbivore distribution/abundance is a major factor determining the abundance of large carnivores on a broad scale (East 1984; Ritchie & Olff 1999; Carbone & Gittleman 2002). However, at a fine scale, our analysis shows that a significantly greater number of kills take place in areas where lions can ambush their prey rather than where prey animals are most abundant. Therefore, prey catchability should be considered essential to models of habitat selection by ambush predators (as opposed to herbivores or, possibly, cursorial predators). Predator–prey dynamics are not only a function of behaviour and relative densities, but also of the precise details of a specific habitat. It is possible that identical guilds of predators and prey could have very different dynamics as a result of fine-scale differences in landscape. To develop long-term conservation plans for large carnivores, it is not enough to maintain large numbers of prey; appropriate hunting habitat may also be required.

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Appendix 1: Goodness-of-fit exact test (χ^2_E)

The use of traditional χ^2 goodness-of-fit tests in resource-selection studies has been criticized. The probability of committing a Type I error increases, especially when availability has been estimated from a small sample with large error margins (Thomas & Taylor 1990).

The premise behind this test is that observations are compared to a distribution of χ^2 values that are based on the expected probabilities from the study, rather than to the standard χ^2 distribution (i.e. a Bayesian style approach (Ellison 1996)). The advantage is that the test is tailored to the data, and therefore small expected values do not bias the outcome to the same extent as the traditional χ^2 test, thus decreasing the chance of a Type I error. The code was written by Dolph Schluter (personal communication). It can be run as a function (called gofsim) in S-plus.

STEPS OF THE CODE

1. obs = the number of observations in each category (in this example there were six categories; category 1 has 37 observations, etc.). expf = the expected number of observations for each category (in this example, category 1 was expected to have 40 observations, etc.).

2. The code calculates the observed χ^2 statistic (chisq) from obs and expf.

3. The code generates a new set of observations (newobs) using probabilities calculated from the expected values (expf). This is a random sample based on the expected frequency and sums to the total number of observations (nobs).

4. The code then calculates a new χ^2 value (newchisq) from the new set of observations (newobs) and the expected values (expf).

5. Steps 3 and 4 are repeated a specified number of times (nsim). The number of simulations (nsim) should exceed 10 000 to ensure a good estimation.

6. A distribution of the 10 000 new χ^2 (newchisq) values (referred to as χ^2_E) is generated. The observed χ^2 value is compared to this χ^2_E distribution which is tailored to the data.

7. Using this new χ^2_E distribution, the code calculates the fraction of simulated 10 000 χ^2_E that exceed the observed χ^2. This is the *P*-value.

8. Reject H_O if $P \leq 0{\cdot}05$. In this paper, we compare the effects of five habitats, therefore H_O was rejected if $P \leq 0{\cdot}05/5 = 0{\cdot}01$ (i.e. a Bonferroni correction for multiple comparisons).

THE CODE

```
gofsim < – function (obs = c(37,6,3,7,6,5), expf =
c(40,18·9,2·7,1·4,0·9,0·1), nsim = 10000){
   nobs < – sum(obs)
   nexp < – sum(expf)
   if(nobs! = nexp) stop(message = 'number of obs and
exp must be equal')
   result < – list()
   dist < – numeric(nsim)
   chisq < – sum(((obs-expf)^2)/expf)
   expfrac < – expf/nobs for(i in 1:nsim){
   z < – runif(nobs)
   newobs < – hist(z,breaks = c(0,cumsum(expfrac)),
plot = F)$counts newchisq < – sum(((newobs-expf)^2)/
expf)
   dist[i] < – newchisq}
   result$chisq < – chisq result$Pvalue < – length(dist[dist
> = chisq])/nsim return(result)}
```