CHAPTER 13

Ranging behavior of orangutan females and social organization

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13.1 Introduction

An animal's home range is the area that it uses in its normal movements. It usually visits all of its range at least once a year, although in some long-lived animals with longer-term fluctuations in food availability and distribution, all parts of the range may not be covered every year (Jolly 1985). If part of the home range is advertised and defended against intruders and thus used more or less exclusively, this part is often referred to as the territory (although definitions vary). Some parts of a home range are often used more intensely than others, and the part used most intensively is often called the core area, although there is no firm and universally agreed upon definition.

It is generally assumed that the size and other features of home ranges are determined largely by ecological factors, such as the density of food (Cowlishaw and Dunbar 2000) and the spatiotemporal distribution of essential resources (usually food, but sometimes water or shelter: Altmann [1974]). To examine these ecological influences in largely solitary species, such as orangutans, we must focus on the home ranges of adult females (the 'ecological' sex: Trivers [1972]), because we can safely assume that male range use is largely a response to the distribution of females in orangutans, just as in most other mammals (see Chapter 17). Fundamental questions about female home ranges therefore concern the determinants of their size, their overlap, the pattern of their use (presence and size of distinct core areas), and the degree to which they are defended. In addition, given the focus of this book, an interesting question is whether there is meaningful geographic variation in these features. These questions are the subject of this chapter.

13.2 Female home ranges

Over the past three decades, various estimates of female home ranges have been published (see Chapter 17 for male home ranges). In Table 13.1 we have compiled the estimates available to date. There is considerable variation between sites in published estimates of female home range size, with the largest estimates of female range size being 15 times greater than the smallest. Despite this variation, however, all studies agree that at each particular site male ranges are larger than those of females.

We must first address the question of whether the observed differences in home range are real or an artifact of varying methods, size of study areas, or duration of study. We will conclude they are real, prompting us to ask what causes this variability. Visual inspection suggests two interesting trends. First, there is indeed variation among subspecies, with *Pongo pygmaeus morio* having the smallest ranges, *P. p. wurmbii* intermediate range sizes, and *P. abelii* having the largest. Second, even within subspecies large variation remains that can be linked to habitat heterogeneity. We will discuss these issues in turn.

Differences in (estimated) home range size reported by different researchers could be due to variation in methods, the size of study areas or the length of study periods. First, all home range estimates presented in Table 13.1 are based on minimum convex polygons around plots of range use (or smoothed versions of convex polygons: cf. Kenward [1987]), suggesting no obvious effect of differential data analysis. Second, some early studies may have had study areas that were too small, so individual

Table 13.1 Best estimates of home range size of female orangutans at various study sites, arranged by subspecies

Study site	Island subspecies	Habitat mosaic	Density individual/km²	Study area size ha	Study duration months	Home range ha
Lokan	B-*m*	Homogeneous	2.1	390 up to 2070	25	65
Mentoko-1	B-*m*	Homogeneous	2.0	300	15	40–60
Mentoko-2	B-*m*	Homogeneous	2.0	300	18	>150
Mentoko-3	B-*m*	Homogeneous	1.0	Unclear	Unclear	>150
Kinabatangan	B-*m*	Homogeneous	2.5–4.0	600	48	180
Tuanan	B-*w*	Homogeneous	4.2	500	24	250–300
Sabangau	B-*w*	Homogeneous	2.0	900	24	250–330
Tanjung Puting	B-*w*	Heterogeneous	3.0	3500	48	350–600
Gunung Palung	B-*w*	Heterogeneous	3.0	2100	103	600
Ketambe-1	S	Homogeneous	5.5	150	38	150–200
Ketambe-2	S	Homogeneous	4.5	350	48	300–400
Suaq Balimbing	S	Homogeneous	7.0	500, up to >2000	52	>850

B-*m*, Borneo *P. p. morio*; B-*w*, *P. p. wurmbii*; S, Sumatra.

Lokan, Horr 1975; Mentoko-1, Rodman 1988; Mentoko-2, Mitani 1989; Mentoko-3, Suzuki 1992; Kinabatangan, Ancrenaz and James unpublished; Tuanan, Tuanan orangutan project Universitas Nasional Jakarta—University of Zürich, Switzerland; Sabangau, Morrogh-Bernard, unpublished data; Tanjung Puting, Galdikas 1988; Gunung Palung, Knott *et al.* in press; Ketambe-1, Rijksen 1978; Ketambe-2, Ketambe orangutan project Universitas Nasional Jakarta—Utrecht University Netherlands; Suaq Balimbing, Singleton and van Schaik 2001.

orangutans spent some of their time outside the study areas. These studies may have underestimated the time females spent outside the regular study area and the surface area they covered during their absences. However, this problem really only potentially affects two studies (Ketambe, Rijksen 1978; Mentoko, Rodman 1988), and for both sites more recent estimates are also available. Third, perhaps the most important cause of differential estimates is duration of study, since home range size estimates do continue to increase as more years of observation accumulate, due to longer-term fluctuations in food supply due to masting (see Chapter 6) and long reproductive cycles (see Chapters 5 and 12). For example, whereas Rodman (1988) suggested female ranges at Mentoko were 40–60 ha, later studies at the same site inferred ranges at least three times as large: over 150 ha (Mitani 1989; Suzuki 1992). Among the early estimates, the one of Galdikas (1988) was the highest and based on the longest study. However, all recent estimates are based on multiple years of extensive follows, and yet variation remains large. Overall, therefore, if we ignore the two early studies based on small study areas, the variation appears largely real and not due to artifacts of methods or sample size.

The values reported in Table 13.1 are the mean values of 'best estimates', i.e. values that may be somewhat larger than the ones actually derived using the polygon method, when there were good reasons to believe that these polygons excluded some areas that are included in the range (usually because females sometimes left the study area). Females within a population may vary in their home range size (see Fig. 13.1 for an example), but we are not trying to explain this variability here, focusing instead on the variation between sites.

13.3 What causes variation in home range sizes?

13.3.1 Ecological heterogeneity of habitats

Some sites produce much higher home range estimates than others, even compared with sites harboring the same (sub)species: Suaq versus

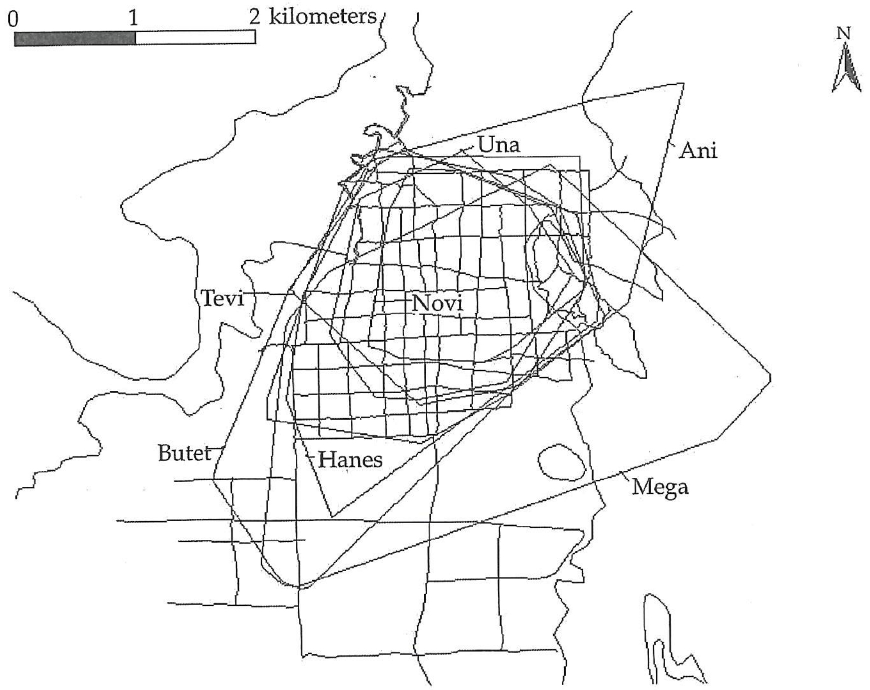

Figure 13.1 Polygon ranges of those adult females known to use most or all of the original study area at Suaq to illustrate the high degree of range overlap.

Ketambe in Sumatra, and Gunung Palung, and to some extent Tanjung Puting, versus Sabangau and Tuanan, all in Kalimantan in the range of *P. p. wurmbii*. The most likely explanation for this variation is ecological heterogeneity of the habitat.

The large home range sizes of both sexes of orangutans at Suaq Balimbing are remarkable in light of the fact that the orangutan density at Suaq is also the highest on record (circa 7 km^{-2}; van Schaik *et al.* [1995]). Because local orangutan density is correlated with estimates of food abundance (van Schaik *et al.* 1995; Singleton 2000; see also Dunbar 1988), the absence of a clearly negative relationship between orangutan density and home range size (Table 13.1) suggests that an additional focus on the distribution, and not merely the density, of resources is warranted. Thus, areas may differ in the spatiotemporal distribution of food, and careful phenological studies of multiple sites are needed.

The Suaq, Gunung Palung and Tanjung Puting study sites all have in common that they contain multiple, quite distinct habitat types, all including both swamp and dryland forests, sometimes of more than one distinct type, in a mosaic on a scale that can be covered by individual orangutans within at most one or two days' travel. Singleton and van Schaik (2001) showed that all females studied at Suaq included all of the main habitat types (riverine, back swamp, transitional peat swamp, and hill forest) into their home ranges (even though only the very edge of the hill forest is used regularly; the animals go higher up only during masting events). They also tended to move from one habitat type to the other as major fruit trees or habitat-wide fruit availability shifted over time, thus gradually covering a larger range than those found at other sites. Likewise, the study area at Tanjung Puting contained swamp forest, dipterocarp forest and heath forest, and at Gunung Palung seven distinct habitat types are found. Tuanan and Sabangau, on the other hand, are more homogeneous peat swamp forests, without major gradients on a scale that can be covered by the slow-moving orangutans within one or two days. Note that the heterogeneity of the habitat is not directly linked to the predominant type of habitat, but rather to the spatiotemporal patterning in food supply, which is usually linked to variation in flooding depth or elevation. Thus, dryland forest without swampy parts and major elevational variation will usually be fairly homogeneous from the orangutan's perspective.

A detailed analysis of tree phenology at Suaq (Singleton and van Schaik 2001) showed that intraspecific fruiting synchrony was high, so the need to have large ranges could not be accounted for by the animals having to search for different trees of the same main species in the diet. Instead, the dominant fruit species in the diet tended to vary from month to month, and their centers of distribution were quite heterogeneous, especially between habitat types, but also within the peat swamp. The orangutans thus moved around their home range to benefit from local peaks in fruit abundance, which were created by different species in the different forest parts.

Swamp forests have much lower floristic diversity than dryland forest (Whitmore 1984). Indeed, the orangutan diet at Suaq contains 61 plant species (van Schaik and Singleton, unpublished data), of which only about 40 occur in the swamp forest. The swamp forests at Tuanan and Sabangau are more diverse than Suaq, with *c.*125 and 135 tree species in their plots (as opposed to some 60 at Suaq), but they are still far less diverse than typical lowland forest sites—usually over 200 species in a 2–3 ha plot, i.e. comparable to the size of the plots used in these swamp forests (Whitmore 1990). Accordingly, in long-term studies elsewhere many more different food species were reported (see Chapter 9). It is therefore likely that a separate swamp effect on home range size exists, i.e., that ranges in swamps are generally larger than in dryland forests; the entries in Table 13.1, while not conclusive given the limited sample size, support this contention.

13.3.2 Subspecies membership

Accepting that some early studies had range size estimates that were too low, and therefore relying only on the later estimates for those sites (Mentoko, Ketambe), we see that the estimates at both sites for *P. p. morio* both less than 200 ha regardless of habitat, are clearly lower than those for the other subspecies. Moreover, if we compare the ecologically more homogeneous sites (see above) Sabangau and

Tuanan, containing *P. p. wurmbii*, with Ketambe, containing *P. abelii*, it seems that the Sumatran females have the largest home ranges. If it is true that in swamps home ranges tend to be larger than in nearby dryland forests, the subspecies differences noted above becomes even stronger, because the ranges in the swamps of Tuanan and Sabangau would have been expected to be larger than those in the dryland forest of Ketambe. The same subspecies difference is found if we compare the two ecologically more heterogeneous sites in the range of *P. p. wurmbii*, Gunung Palung and Tanjung Puting, with Suaq in the *P. abelii* range. Thus, from *P. p. morio*, to *P. p. wurmbii*, to *P. abelii* we see a gradual increase in home range size, even if we control for the ecological heterogeneity of the local habitat.

13.4 Features of home range use

Females apparently do not use all parts of their home range evenly. Indeed, Knott *et al.* (in press) show that they spend 50% of their time in only 13% of their home range, i.e. they have core areas of 65 ha on average (using 200 × 200 m grid cells to estimate the area in which 50% of time is spent). A similar exercise for Suaq (Singleton and van Schaik, unpublished) shows a similar picture, with core areas between 44 and 80 ha (for Ani and Mega respectively, the females whose home ranges were largely within the study area), again in the order of 10% of their range. Since in these cases search effort is not evenly spread throughout the females' home ranges, these core area estimates may be seriously biased toward the lower end, especially at Suaq, where many focal follows began at the boardwalk as the animals were often first encountered there. Still, these figures show that use of the home range seems to be highly uneven. At Suaq, for instance, females only made 'excursions' into the hills during mast fruiting periods. Although one might expect core areas to be relatively larger in sites with more homogeneous habitats, preliminary data from Sabangau do not support this idea. A single female there spent 50% of her time in only 6% of her home range, approximately 20 ha. However, to obtain a better feel for the size of core areas and their variation, many more analyses are needed and measures of the degree of bias must be developed.

Overlap of female home ranges appears to be a common trait at all sites, albeit to highly varying degrees. In the absence of quantitative analyses of home range overlap for many sites, an easily estimated measure of overlap is the number of home ranges found to contain a given (usually rather centrally located) point within a study area. Table 13.2 shows the overlap for various study areas. Large variation is found, which largely reflects density and mean home range size. Range overlap appears highest at the sites with the most heterogeneous habitats: within Borneo, overlap is higher at Gunung Palung than at Tuanan and Sabangau, and within Sumatra, at Suaq than at Ketambe. Density may play an additional role, given the high overlap at Suaq.

In general, it is clear that at high overlaps, there is no overall home range territoriality. Knott *et al.* (in press), however, argue that core areas can be considered territories because mutual avoidance

Table 13.2 Female range overlap at several sites, expressed in number of female home ranges containing a given point in the center of the study area (to avoid cul-de-sac phenomena)

Study site	Adult female overlap	Reference
Suaq Balimbing	16	Singleton and van Schaik 2001
Ketambe	5–8	Ketambe orangutan project Universitas Nasional Jakarta—Utrecht University Netherlands—SOCP
Gunung Palung	At least 6	Knott *et al.* in press
Sabangau	4	Morrogh-Bernard, personal communication
Tuanan	4	Tuanan orangutan project Universitas Nasional Jakarta—University of Zürich, Switzerland
Kinabatangan	4	Ancrenaz and James personal communication

SOCP, Sumatran Orangutan Conservation Programme.

results in passive range exclusion in the most heavily used parts of the home range. Although there is little evidence for active defense of these territories, resident females are more likely to win fights within their own core area, which is also suggestive of territoriality. This is consistent with the observations at Suaq that females make excursions into the hills especially when there is abundant food there, although they still avoided encounters with possible residents there (Singleton 2000). Likewise, observations from Tuanan show that females withdraw into their core areas during times of food scarcity (van Schaik, unpublished data).

With respect to temporal stability, home ranges were found to be fairly stable at Suaq (Singleton and van Schaik 2001), as they were at Cabang Panti in Gunung Palung and at Kinabatangan (M. Ancrenaz and S. James, unpublished data), although degree of stability has not yet been compared quantitatively. Shorter-term data from Sabangau and Tuanan suggest similar range stability. Anecdotal observations from Suaq and Tuanan suggest that adult females who lost part of their home range to forest destruction, nonetheless did not abandon or move their ranges. The stability of nest numbers over time at Suaq, despite intensive logging in nearby areas (van Schaik 2004), supports this interpretation. If confirmed, these observations suggest a strong tendency to remain in their home ranges, come what may. The strong loyalty to the core area may be a way to maximize resource acquisition through avoiding competition over resources with neighboring females (Knott *et al.*, in press).

13.5 Day journeys

Table 13.3 shows that the average daily travel distances are shortest for females of *P. p. morio*, whereas those of the other taxa are approximately similar. Apart form the small Sabangau sample sexually active females cover larger distances each day at some sites than the other adult females (Utami Atmoko 2000), although the differences are modest (van Schaik 1999). Females at ecologically more heterogeneous sites appear to have similar day journeys to those at more homogeneous sites. Thus, females do not need to increase their mean daily path length to switch between habitat patches. These switches can generally be made with journeys that do not exceed the normal day range.

13.6 Female clusters

Singleton and van Schaik (2002) showed that females at Suaq formed distinct clusters. Cluster members had home ranges that overlapped widely, showed preferential association (controlling for home range overlap) and reproductive synchrony, and were thought to consist of close relatives. Figure 13.2 illustrates this pattern with data from simultaneous follows, showing that northern and central females were closer to other females of their own cluster (mostly while not in actual association).

Recent results from Gunung Palung (Knott *et al.* in press) are consistent with this picture. Female relatives show greater home range overlap than non-relatives and encounter each other

Table 13.3 Daily path lengths of adult females at different sites (with standard deviations in parentheses)

	Mentoko (Kutai)	Kinabatangan	Sabangau	Tuanan	Tanjung Puting	Gunung Palung	Suaq Balimbing	Ketambe
Island and subspecies	B-*morio*	B-*morio*	B-*wurmbii*	B-*wurmbii*	B-*wurmbii*	B-*wurmbii*	S	S
Sexually active females	[305]	162	769	1025 (471)	711	690	1077 (368)	722 (293)
Mothers			809	766 (355)			833 (306)	675 (282)

Where possible, sexually active females and mothers with dependent infants were entered separately.

Mentoko, Rodman (1977), mean value for flanged males and adult females; Sabangau, Morrogh-Bernard unpublished data; Tuanan, Tuanan orangutan project Universitas Nasional Jakarta—University of Zürich, Switzerland (795 days total); Tanjung Puting, Galdikas 1988; Gunung Palung, Knott unpublished data; Kinabatangan, KOCP unpublished data; Suaq Balimbing, Suaq Balimbing orangutan project Universitas Indonesia Jakarta—Duke University USA; Ketambe, Wich *et al.* 2006b.

preferentially. Although cluster analysis of preferential association at Gunung Palung has not yet been carried out, these results are highly suggestive that there is preferential social affiliation between some adult females and this pattern may extend to other adult females at Gunung Palung. The data from these two sites complement each other to form a suggestive picture of female clusters across subspecies. The known genetic relationships at Gunung Palung counterbalance the lack of known genetic identity of the female clusters at Suaq; the presence of known clusters at Suaq highlights the potential significance of the preferential encounter rate among related females at Gunung Palung.

These results confirm the philopatric tendencies of female orangutans (see Chapter 12). At Tuanan, a mother was seen to interfere when her maturing daughter was attacked by another adult female (M. van Noordwijk, personal communication), although no such observations have been reported from other sites. This also suggests that settling near one's mother can be advantageous for young females, although this may not always be possible (cf. Knott *et al.* in press).

13.7 Discussion

13.7.1 Variation in home range size

We found two main patterns in home range size, one linked to habitat heterogeneity (and perhaps population density) and a second, independent one linked to taxonomic affiliation.

Some of the largest home ranges were found in areas with the highest orangutan density, contrary to a naive ecological expectation that overall productivity would determine home range size. The best explanation for this anomaly is the spatial 'grain' of the mosaic of forest types, i.e. the mean distances between patches of different floristic composition and thus of different peaks in food availability. This grain is not easily recognized from simple habitat analysis, because it may sometimes depend on the distribution of one or two main food species, but is revealed by orangutan movement patterns. Thus, in Suaq, Gunung Palung or Tanjung Puting home ranges must be large, over 500 ha, to allow access to all of the top species in the diet. Elsewhere, as in most dryland forests, the 'grain' is very different, due to the much higher species densities (number of species per unit area), and fine-grained patchiness in species distributions due to small-scale topographical variation, for instance due to streams and hills. Thus, an orangutan moving about in this habitat may find a different phenology at a short distance, within a home range of about 200 ha, the size observed in some studies. Moreover, moving longer distances does not bring the female into a radically different habitat or phenology, making it futile to move over longer distances. This fine habitat grain allows

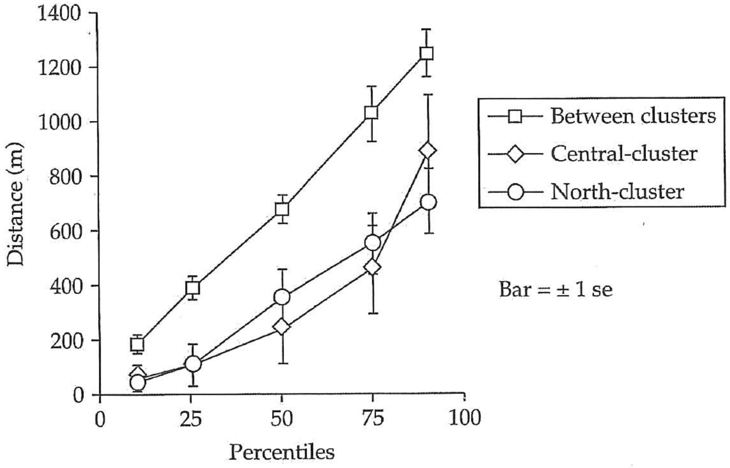

Figure 13.2 Cumulative distance distributions between females of the same or different clusters at Suaq Balimbing, based on simultaneous follows. Some of these follows were made while the females were in association.

females to survive in smaller areas, albeit generally at lower densities and with less overlap due to reduced overall productivity. On this argument, habitat heterogeneity should not affect daily travel distance, which indeed it did not.

In addition to the distribution of food resources, population density may play an additional role in explaining variation in female home range size. High population density and patchy resources should increase the amount of scramble competition for food, to which orangutans respond by increasing their home range size (Knott *et al.* in press). Indeed between-unit scramble competition is often thought to be a reflection of population density (van Schaik 1989), and as the number of females overlapping a particular female's range increases, so may the need to enlarge home range size. For instance, Singleton and van Schaik (2001) suggest that the low species richness of the Suaq swamp results in a clumped distribution of fruiting tree species at any given time, leading the orangutans there to use a larger area to maintain an adequate diet. However, the role of scramble competition cannot be very large, because the females at Suaq spend much of their time in association with each other (provided they belong to the same cluster; see below), which is not expected if scramble competition drives them apart.

The second pattern in home range sizes noted was the gradient of increasing female home range size from *P. p. morio* in the east to *P. abelii* in the west. The eastern *P. p. morio* also had by far the shortest daily travel distances. The degree of reliance on non-fruit fallback foods such as leaves and inner tree bark provides a ready explanation for this gradient. Both Fox *et al.* (2004) and Wich *et al.* (2006a) showed that Sumatran orangutans maintain a high level of frugivory at all times, whereas the degree of frugivory fluctuates much more in Borneo, with the eastern *P. p. morio* populations showing the most extreme variation (see also Chapter 8). Thus, the most frugivorous orangutans need the largest home ranges, which therefore also show the highest overlap (see above). Obviously, this trend is reflected at higher taxonomic levels as well, where frugivores live in larger home ranges than folivores (Clutton-Brock and Harvey 1977), which can fall back on foliage during times of fruit scarcity.

13.7.2 The female component of social organization

The more recent long-term studies support the idea that related females form clusters, showing that orangutans live in more than mere neighborhoods, just like other primates. The data also suggest a pattern in cluster size across sites, in which larger clusters are found at sites with higher densities, and almost certainly higher overlap in home ranges, including core areas.

The parallel results from Gunung Palung and Suaq suggest that large range size tends to be accompanied by high overlap and larger size of the female clusters. Clusters arise when daughters or sisters of particularly productive females settle in adjacent ranges. Clusters can be recognized more readily where these female relatives can settle in ranges that largely coincide, i.e. in those sites where home ranges must be large, because in these conditions opportunities for association of more than two females are much more common.

Relationships among females that are members of different clusters are not friendly. Observations at Gunung Palung suggest that females are more likely to win fights within their own core areas than elsewhere in their home range, but it is not yet clear whether this also holds elsewhere.

13.7.3 Future work

This review has revealed suggestive relationships between home range size, frugivory and habitat heterogeneity, between home range overlap, female cluster size and frugivory, and perhaps between home range size, food competition and population density. However, we need more quantitative work on all these variables from several sites before we can consider these trends well established. In particular, in order to identify the determinants of home range size, we need quantitative data on the habitat mosaic and inter-annual variation in food availability for multiple sites.

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