Climatic effects upon foraging success and population changes of female Greater Horseshoe Bats

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Klimatische Auswirkungen auf Jagderfolg und Populationsveränderungen bei den weiblichen Großen Hufeisennasen

Effets climatiques sur le succès de chasse et les changements d'effectif des femelles du grand Rhinolophe

Introduction

The urgent need to conserve the declining populations of Greater Horseshoe Bats in many European countries makes it imperative that all factors influencing its population dynamics are fully understood. There can be little doubt that a viable population can only be sustained in a region if a combination of situations exist. These include a suitable secure warm summer roost, or range of roosts close together, within favourable foraging habitat for a distance of some 2.5 km (JONES, DUVERGÉ & RANSOME 1995); numerous undisturbed hibernacula within a 40 km radius of the summer roost, offering a range of temperatures and air-flow conditions, surrounded by suitable foraging habitat to allow winter feeding (RANSOME 1968, 1971), and a mild summer climate of sufficient duration to allow time for successful reproduction and growth to occur (McOWAT & ANDREWS 1994, RANSOME & McOWAT 1994, JONES, DUVERGÉ & RANSOME 1995, RANSOME 1995). Detailed long-term population changes for conserved and protected sites indicate that numbers remain remarkably stable for many years, but can show dramatic declines associated with prolonged severe climate (RANSOME 1989). Recovery from such declines is a very slow process. Understanding the mechanisms behind these events is an important prelude to possible prevention or mitigation of future crashes likely to threaten extinction in a region. This paper investigates the impact of severe weather upon the feeding success of female Greater Horseshoe Bats at different phases of summer reproduction, and summarises published studies of the effect of climate upon their survival and hence population changes.

Methods

Study area and methods used:
A small population of about 45 breeding females in a total population of some 180 individuals born at the Woodchester Mansion breeding site, at the northern limits of the species' distribution (latitude 52° N), was studied (RANSOME 1989). Female reproductive condition was determined from the state of the mammary glands, their nipples, and that of the pelvic false teats during captures made in the breeding attic (RANSOME 1995). From 1986 to the present, captures of mothers carrying their young allowed the parturition timing of specific females to be identified. The young's birth date is identical to its mother's parturition date for the year in question. In the text birth date is used with reference to the young, or to mother and young if it applies to both. Parturition date refers only to mothers. Feeding success from dawn foraging was estimated as total mass of dry faeces produced per dawn feed. Estimates were made using collections of faecal pellets from individuals bagged separately after early morning capture on various days (n = 13) in the summers from 1990 to 1994. Method details are provided in JONES, DUVERGE & RANSOME (1995). Detailed weather data was collected 9 km from the breeding site. Dawn weather was broadly classified into three types: good weather (temperature >8° C; no rain; low wind speed); cold weather (temperature <6° C; no rain; low wind speed) and wet/windy weather (temperature >8° C; heavy continuous rain with high wind speed). As breeding site captures had to be arranged well in advance, the weather conditions affecting foraging could not be selected. This resulted in small sample sizes for cold and wet/windy weather conditions. All statistical calculations were carried out using MINITAB version 8.21.

Results

Foraging success of female Greater Horseshoe Bats in normal weather conditions:
Table 1 shows the mean estimated dropping production (MEDP) from dawn foraging per female bat in mg for each month from June to September during good weather. MEDP shows considerable changes, with the lowest level in June, and high levels in July and August. Table 2 shows the effect of growth and reproductive state upon MEDP during good weather. All data samples were normally distributed. Oneway ANOVA showed that there were significant differences between the means (F_{2s3} = 35.01, $p < 0.001$). Tukey tests showed significant differences ($p < 0.05$) exist between the means for lactating females and those of all other females, and between immature females and non-breeding females, but not between the other means.
These data support the hypothesis that, in good weather conditions, the reproductive phase itself, rather than the period of the summer, is the major influence on estimated dropping production (EDP), especially since mean data for lactating females are almost constant in July and August (501.7 mg, ± 141.1 s.d., n = 89; 502.7 mg, ± 159.8 s.d., n = 26, respectively). Production is greatest during lactation, followed by immaturity.

early post-lactation, late pregnancy and non-breeding, although differences between the last three groups are not significant. MEDP by lactating females is about twice that of late pregnant females.

The impact of severe weather upon EDP by females:
Figure 1 shows the impact of severe weather upon EDP levels by immature and lactating female bats. Table 3 summarises data for cold weather and wet/windy weather separately, and combined as severe weather. Since severe weather EDP data sets were not normally distributed (fig. 1), nonparametric methods were used to find the effect of severe weather on EDP medians. KRUSKAL-WALLIS tests showed that the median for lactating females in good weather was significantly different ($p < 0.001$) from those in cold and wet/windy weather, but not between the types of severe weather ($p = 0.617$, NS). Data for the two types of poor weather conditions were therefore combined as severe weather. Mann-Whitney tests were carried out to compare EDP after good and severe weather by the three groups of females for which data were available (immatures, lactating and early post-lactating females). All three groups showed significantly reduced medians in severe weather compared with good weather ($p < 0.0003$ in all cases). A. KRUSKAL-WALLIS test comparing EDP data among immature, lactating and early post lactating females in severe weather showed no significant differences existed between their medians ($p = 0.413$, NS).

Discussion

Food consumption by females in good weather:
EDP is a measure of an individual's foraging consumption, from the previous dawn feed because digestion and egestion are very rapid in bats. Greater Horseshoe Bats egested most (70%) of their faeces within 4.5 to 9 hours of being fed 1 to 4.5 g of insect food (RANSOME 1978). EDP is probably the only possible method of estimating foraging success which does not harm the bats. Its reliability should suffer from any variation in the rate of digestion by individuals, and any effects such as dietary switches, which may alter the mass of insect exoskeleton in the faeces. These points were not addressed in the present study. We should therefore probably not pay too much attention to small differences between data, or statistics derived from them. Nevertheless, this preliminary study shows that the consumption levels of lactating females in good weather are considerably greater than those of all other females, presumably because lactation poses the highest energy and nutrient demands upon females (ANTHONY & KUNZ 1977, BARCLAY 1989). Late-pregnant females showed about 50% of the consumption of lactating females, and this difference accounts for the low levels of all females combined, seen in June (table 1), and also for the whole colony at that time (RANSOME 1973). Immature females were the second highest consumers, probably due to the fact that they are still showing growth in lean body mass (RANSOME 1995).

The effect of severe weather upon food consumption by females:
The significant additional consumption by lactating females over other female groups disappears in severe weather, when mean and median levels for all females assessed fall dramatically. There is considerable individual variation in this reduction, with some females maintaining quite high levels. This may be due to differences in foraging efficiency, circumstances at specific feeding sites such as shelter, or variable motivation among females. Whatever the reasons are, the effect of severe weather at any stage of the summer is to erratically reduce or totally deprive a female of energy and nutrients. This is especially critical for lactating females as body reserves are limited (HARRISON-MATHEWS 1937) and likely to last for only one or two days (SPEAKMAN & RACEY 1987). The latter authors felt that body reserves were only capable of being used to insure against erratic short-term variation in food supplies.
Insect availability is considerably influenced by weather effects, especially temperature (TAYLOR 1963, JONES, DUVERGÉ & RANSOME 1995) and is known to affect colony faecal production in spring (RANSOME 1973). The present study shows cold and/or wet/windy weather are significant events reducing consumption by bats throughout the summer, confirming the observations on the effect of climate on feeding activity by RYDELL (1989) for *Eptesicus nilssoni*.

Climatic effects upon populations:
The present study adds to our understanding of climatic effects on population changes in this species by demonstrating that weather conditions may affect food consumption at any time of the summer. Cold conditions are particularly likely to affect dawn foraging. A poor spring climate delays births by extending pregnancy (RACEY 1973). A 2° C fall in mean April plus May temperature delays mean birth date by 18 days (RANSOME & McOWAT 1994). The mean birth date in a particular summer is crucial since it affects the subsequent survival of both the cohort born that year and its mothers (RANSOME 1989, 1995). The later the births, the lower the survival rates of both groups. Mean birth date is also negatively related to the productivity of young from those that manage to survive to become breeders. Since parturition dates are latest in young mothers they experience the highest mortality rates after severe spring and summer climates. The loss of many young and vigorous females, alters population demography, and is a major factor delaying recovery for many years by removing reproductive potential (RANSOME 1995). It adds to the effects of altered sex ratios favouring male births (RANSOME & McOWAT 1994), years without breeding, the high mortality of that year's cohort of female young, and the low fecundity of any survivors (RANSOME 1995).

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Summary

Food consumption by female bats after good weather, estimated as dry faecal production after dawn foraging, showed wide variation among reproductive groups, and individuals within those groups. Consumption was significantly higher for lactating females than for all other groups, and immature females consumed significantly more than non-breeding females. The lowest consumption was shown by non-breeding females. Consumption by lactating, early post-lactating and immature females was greatly reduced by both cold (<6° C) and wet/windy weather throughout the summer. Such severe summer weather, if prolonged, has major effects upon long term population changes by affecting various parameters such as survival and breeding rates, population demography, sex ratios and fecundity. Many of these factors operate via birth timing.

Zusammenfassung

Die nach schönem Wetter von weiblichen Tieren verzehrte Nahrung, nach der Morgenjagd vermutlich als Trockenkot ausgeschieden, war unter den Wochenstubengruppen, aber auch unter den einzelnen Tieren innerhalb dieser Gruppen sehr unterschiedlich. Für säugende Weibchen war der Verzehr bedeutend höher als bei allen andern Gruppen, und unreife Weibchen verzehrten wesentlich mehr als nicht mit der Aufzucht beschäftigte Tiere, die den niedrigsten Verzehr aufwiesen. Der Verzehr von säugenden und unreifen Weibchen sowie von Weibchen unmittelbar nach der Laktation war während des ganzen Sommers wegen kalten (<6°C) und nassen, windigen Wetters stark herabgesetzt. Solch rauhes Sommerwetter hat bei anhaltender Dauer große Auswirkungen auf Langzeit-Populationsveränderungen und beeinflußt verschiedene Parameter wie Ueberleben und Fortpflanzungsraten, Populationsdemografie, Geschlechterverhältnis und Fruchtbarkeit. Viele dieser Faktoren wirken sich über den Geburtenzeitpunkt aus.

Résumé

En ce qui concerne la consommation de nourriture des femelles après beau temps, sécrétée après la chasse matinale probablement sous forme d'excréments secs, il y avait de grandes différences parmi les groupes de reproduction, mais aussi parmi les individus de ces groupes. La consommation était notamment plus élevée pour les femelles allaitantes que pour tous les autres groupes, et les femelles impubères consommaient bien plus que les femelles non nourrissantes. La plus basse consommation résultait pour les femelles non nourrissantes. La consommation des femelles allaitantes et impubères ainsi que celle des femelles immédiatement après la lactation étaient fortement réduites tout l'été en raison du temps froid (<6°C) et humide/éventé. Ce mauvais temps d'été, surtout lorsqu'il se maintient, peut avoir des effets graves et entraîner des changements de population à long terme tout en affectant différents paramètres tels que survivance et taux de reproduction, démographie, rapport des sexes et fécondité. Beaucoup de ces facteurs s'expriment en fonction du moment de naissance.

All growth and reproductive states combined, except young of the year. MEDP is mean estimated dropping production, measured as dry mass in mg per bat from dawn foraging. Good waether means no rain, light wind and temperature > 8 °C.

month of summer	sample n	MEDP	median	standard deviation
June	21	259.0	245	21.2
July	125	444.9	440	14.8
August	43	455.9	478	26.1
September	65	301.9	305	16.6

Table 1: The effect of time during the summer on mean estimated dropping production by female Greater Horseshoe B ats in good weather

Tabelle 1: Der Zeiteffekt im Sommer auf die geschätzte mittlere Kotproduktion der weiblichen Grossen Hufeisennasen bei gutem Wetter

Table 1: L'effet de temps en été sur la production d'excréments moyenne estimée des femelles du grand Rhinolophe en beau temps

Explanation as for table 1.

reproductive state	sample n	MEDP	median	standard deviation
immature (1, 2 yrs)	51	334.8	324.0	115.5
late pregnancy	20	258.2	245.0	133.6
lactation	125	494.0	481.0	148.5
early post-lactation	48	302.1	273.5	141.6
non breeding adult	10	179.4	161.0	76.2

Table 2: The effect of growth and reproductive condition upon the mean estimated dropping by female Greater Horseshoe Bats in good weather

Tabelle 2: Die Auswirkung von Wachstum und Fortpflanzungsbedingungen auf die geschätzte mittlere Kotproduktion der weiblichen Grossen Hufeisennasen bei gutem Wetter

Table 2: L'effet de croissance et de la condition de reproduction sur la production d'excréments moyenne estimée des femelles du grand Rhinolophe en beau temps

MEDP and weather explanations are as for table 1. All data are medians in mg used in Kruskal-Wallis tests (see text). Figures in brackets are sample sizes. Severe weather is combined data for cold and wet/windy weather.

reproductive state	weather conditions during dawn foraging			
	normal	cold	wet/windy	severe
immature	324.0 (51)	72.0 (7)	48.0 (5)	60 (12)
lactation	481.0 (125)	87.5 (22)	127.0 (9)	98 (31)
early post-lactation	273.5 (48)	67.5 (6)	81.0 (13)	81 (19)

Table 3: The effect of cold and wet/windy weather upon the mean estimated dropping production by immature, lactating and early post-lactating female Greater Horseshoe Bats

Tabelle 3: Die Auswirkung von kaltem und nassem/windigem Wetter auf die geschätzte mittlere Kotproduktion von unreifen, säugenden und seit kurzem nicht mehr laktierenden weiblichen Hufeisennasen

Table 3: L'effet du temps froid et humide/éventé sur la production d'excréments moyenne estimé de femelles du grand Rhinolophe, qui sont impubères, allaitantes et ne plus allaitantes depuis peu

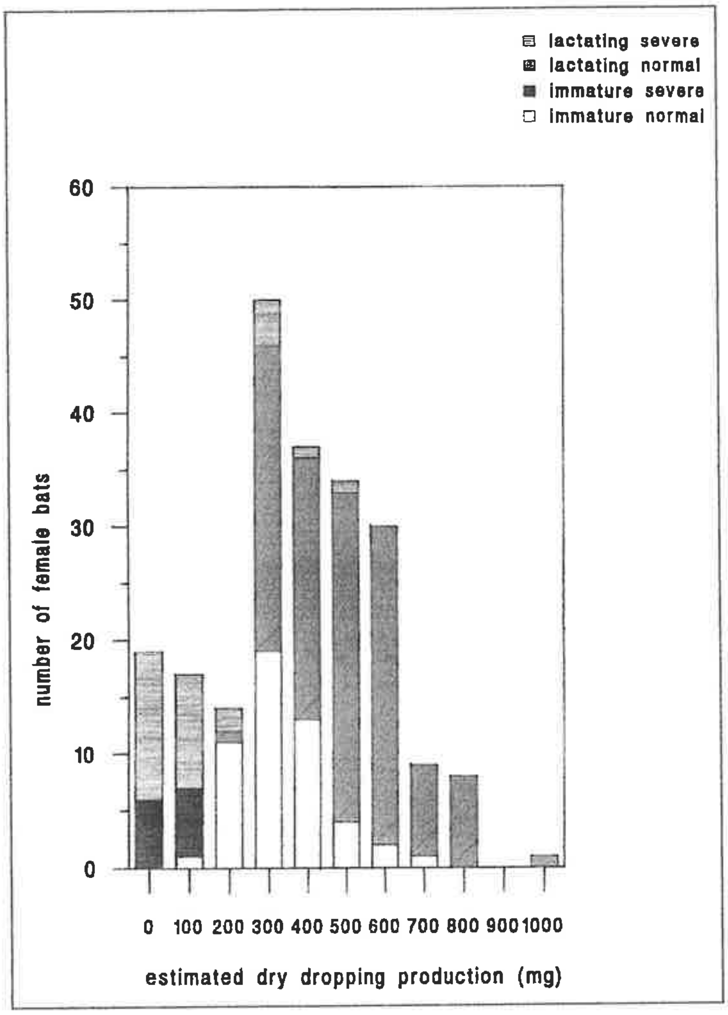

Figure 1: Climatic effects on female bats: Ransome, R.D.

Stacked bar-graph showing the effect of severe summer climate on the frequency distributions of dry faecal production by lactating and immature female bats.
Key: diagonal lines = lactating females, normal weather; horizontal lines = lactating famales, severe weather; white (blank) = immature females, normal weather; cross hatched lines = immature females, severe weather.

Bild 1: Anzahl weiblicher Tiere
Geschätzte Trockenkotproduktion (mg)

Abb. 1: Nombre de femelles
Production d'excréments secs estimée (mg)

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