Effects of supplementary food on density-reduced breeding in an African eagle: adaptive restraint or ecological constraint?

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Increased population density often reduces reproductive output in breeding birds, but the underlying mechanisms (adaptive restraint v reduced food resources) behind decreased productivity are poorly understood. Here I correlatively and experimentally investigated the roles of food, breeding density, latitude, altitude and rainfall in limiting productivity of Wahlberg's Eagles *Aquila wahlbergi* throughout Africa. Breeding success in equatorial and subtropical Africa (0°–30°S) was highly density-dependent but showed no latitudinal or rainfall-related trends. Pairs in dense populations produced half as many young annually as pairs in low-density populations. Density (but not rainfall or latitude) also explained much of the geographic variation in the mean proportion of pairs attempting to breed each year and the incidence of two-egg clutches.

Breeding within populations was consistent with these density-dependent trends: incidence of two-egg clutches increased in a declining population, and productivity was inversely related to breeding density and rainfall combined. To determine if reduced food resources accounted for reduced output in dense populations, eight pairs were food supplemented: supplementary food failed to induce nonbreeding pairs to breed; nor did it induce earlier laying or increase egg size or clutch-size. Population density itself was unrelated to two correlates of food resources, rainfall and latitude. I conclude that population density influences most aspects of breeding in Wahlberg's Eagles, and reduced food resources do not appear to explain these trends. Hence, adaptive restraint may account for decreased annual reproduction in this species.

Numerous experimental studies have supported Lack's (1947, 1954) thesis that food is the most important proximate factor influencing reproduction in birds. Experimentally increased food availability has enhanced fitness-related variables such as laying date (Kallander 1974, Yom-Tov 1974, Smith *et al.* 1980), the incidence of second broods (Brömssen & Jansson 1980, Davies & Lundberg 1985), egg size (Högstedt 1981), clutch-size (Högstedt 1981, Newton & Marquiss 1981, Dijkstra *et al.* 1982, Arcese & Smith 1988) and enhanced post-nestling survival (Boag 1987, Simons & Martin 1990, Hochachka & Smith 1991). In several experimental studies, increased clutch-size and earlier laying occurred simultaneously, leading Meijer *et al.* (1988) to postulate that laying date (not food) was responsible for increased clutch-size in several species. However, in at least three other raptors, larger clutches occurred independently of earlier laying date (Newton & Marquiss 1981, Simmons 1989, Hörnfeldt & Ecklund 1991, Korpimäki & Hakkarainen 1991). Therefore, food resources do appear to influence clutch-size directly in many species.

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Similarly, latitude has been shown to have a profound, but as yet experimentally untested, effect on clutch-size and hatchability (Moreau 1944, Klomp 1970, Ricklefs 1980, Koenig 1982, Jenkins 1991), even allowing for body-size variation (Simmons 1989, Kulesza 1990). However, most of the results apply to passerines (see Moreau 1944). When similar supplementation experiments or analyses have been applied to larger, longer-lived species, less clear cut or nonsignificant results occur. For example, Poole (1985) found no change in laying date or clutch-size for food-supplemented Ospreys *Pandion haliaetus*, and Powell (1983) found no change in the timing of laying and only marginal clutch-size increases for food-supplemented Great White Herons *Ardea herodias*. Moreover, in two latitudinal analyses of clutch-size variation in owls, Murray (1976) found negative trends for six small species but no trend for the large Great Horned Owl *Bubo virginianus*, and Donázar (1990) found no variation for the large Eurasian Owl *B. bubo*. Non-experimental studies of large raptors which contrasted breeding success in areas of differing primary productivity similarly found no significant differences (Hustler & Howells 1988, 1989). While such results may be statistical artifacts of the low variation in clutch-size of large species, they also suggest that factors

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This paper reports on this three-tier approach to determine ultimate factors limiting reproduction in Wahlberg's Eagles *Aquila wahlbergi* in Africa. This small (1300 g) migrant (Steyn 1982, Simmons 1990) is relatively long-lived (mean 6.8 years: R.E. Simmons, unpubl.) and breeds throughout south-central Africa. Eight studies of this common eagle from the equator southwards allowed a latitudinal analysis of reproduction. Simultaneously, marked differences in breeding density and rainfall allowed an appraisal of density-dependent factors and (indirectly) food abundance in Africa. Some birds in the densest known population were then given supplementary food to determine whether limited food resources were constraining output.

METHODS

Study area

I undertook a 4-year study of Wahlberg's Eagle in the subtropical lowveld region (*c.* 300 m a.s.l.) of South Africa, within the Sabi Sand Reserve (24°48'S, 31°23'E). This wilderness area supports broadleaved and *Acacia* woodland savanna on granitic sandveld and clays. Bush clearing and annual burning have resulted in a mosaic of park-like habitats, interspersed by more wooded areas and extensive riverine vegetation, favoured by Wahlberg's Eagles. Rainfall occurs chiefly from October to March, the eagles' breeding season, averaging between 570 and 670 mm per year. Limited hunting of large mammals occurs, but birds are undisturbed. The study area declined from 188.5 km² in 1988 to a 148.5-km² area thereafter (due to poor communications with the Sabi Sabi landowner). Since habitat type and density of pairs were little different in the smaller area (23 v 22 pairs/100 km²) the revision made no difference to density-dependent analyses.

Latitude and density-dependent effects

Eight population studies were reviewed to evaluate the effects of latitude, altitude, population density and rainfall on reproduction throughout Africa: Brown (1955) and Smeenk (1974) for Kenya, Vande Weghe (1979) for Rwanda, Steyn (1962, 1980) for Zimbabwe, Tarboton (1977) and Tarboton & Allan (1984) for north-central South Africa, and Snelling (1969) and this study for northeastern South Africa. Additional data from 7 years' observations were provided by T. McClurg in Natal, South Africa, the southern breeding limit of Wahlberg's Eagle. Population density estimates unreported in Steyn's (1962) study area were provided by R. Hartley (*in litt.*), who studied these eagles in the same area.

Two years of additional breeding data were also provided by Hartley. These studies encompass the entire range of breeding latitudes in southern and central Africa and allow the first assessment of latitudinal effects on reproduction for any eagle.

Population and reproduction assessments

Intensive study of the Sabi Sand population of Wahlberg's Eagles (n = 40 pairs) was undertaken in the 1988 and 1989 breeding seasons (September–March). Thereafter, twice-yearly visits (early October and early January) were made until January 1992. Visits were timed to: (i) assess variation in breeding initiation and egg and clutch-size; (ii) patagially wing-tag and re-sight marked birds and (iii) monitor breeding success of all nests. Migrant eagles arrive on territory in August–September, lay eggs in September–October and fledge young in December–January.

I could verify some findings by determining if similar factors also influenced breeding output in a population of Wahlberg's Eagles studied over 10 years in northern South Africa by W.R. Tarboton (*in litt.*). Details are given in Tarboton & Allan (1984).

To determine research-related disturbance, I recorded in 1988 the number of my nests visits in relation to the incidence of nest failures. Most nests failed before my first visit, so my research activity had minimal effect on eagle productivity. Extendable mirror poles were always initially used to check nest contents and minimize disturbance (Simmons 1993).

To understand reproductive success in relation to rainfall, the proportion of pairs that bred was related to "early" (August–September) rainfall, when birds began nesting. Breeding success was correlated with "late" (October–December) rainfall, when adults were brood-rearing. Precipitation was measured daily by fixed rain gauges in the study area by the park warden.

Thirty-four adult eagles were caught within their nesting territories on rodent-baited bal-chatri traps. Wing-tags with unique colour combinations were pinned through the patagium (Simmons 1991) to allow year-by-year re-identification of individuals in the field. Survival and mate fidelity are reported elsewhere (Simmons 1993). Many nests were first found with the aid of reserve staff, while concealed nests were discovered by plotting known sites on maps and searching the gaps within the regular nest-spacing pattern.

Egg lengths and breadths were measured with vernier callipers to the nearest 0.01 mm, and eggs were weighed with a 100-g Salter balance to the nearest 0.1 g. Volumes (cc) were computed from $V = 0.51 \times$ length (cm) $\times$ breadth² (cm) (Furness & Furness 1981).

Supplemental feeding

To understand the role of food supply in reproduction, eight pairs of eagles (six early and two late arrivals) were supplied

Table 1. *Breeding success and the proportion of breeding pairs from eight Wahlberg's Eagle populations throughout Africa in relation to population density, latitude, altitude and rainfall*

Area (latitude)	Population density (pairs/100 km²)	Average % of pairs breeding	Breeding success (young/breeding pair/year)	Altitude (m. a.s.l.)	Mean annual rainfall (mm)	Source (no. of pairs and years studied)
Embu, Kenya (0°)	2.9	84%	0.63	2500	900	Brown 1955 (11, 4 years)
Tsavo, Kenya (3°S)	1.5	82%	0.78	400	441	Smeenk 1974 (4, 4 years)
Essexvale, Zimbabwe[1] (20.2°S)	4.9	88%	0.65	1200	632	Steyn 1962, 1980 (7+9, 15+2 years)
Steenbokpan, South Africa (23.75°S)	3.8	—	0.64	900	450	Tarboton & Allan 1984 (23, 1 year)
Nylsvlei, South Africa (24.5°S)	5.4	81%	0.57	1100	620	Tarboton 1977 (23, 4 years)
Sabi Sand, South Africa (24.5°S)	22.9	64%	0.31	400	620	Simmons, this study (40, 4 years)
Kruger Park, South Africa (24.5°S)	11.5	80%	0.39	300	525	Snelling 1969 (8, 3 years)
Natal, South Africa (29.8°S)	2.4	—	0.71	600	1000	T. McClurg, in litt. (1, 7 years)

[1] The studies of Steyn (1962, 1980) and R. Hartley (*in litt.*) were combined since they encompassed the same study area: Hartley's unpublished data showed that 85% of 15 pairs bred per year and 9 of 13 breeding birds reared young (69%) in 1986 and 1987.

with extra food in 1988 and 1989 as they appeared at their nest sites following migration. Eggs are usually laid 3–6 weeks after arrival (R.E. Simmons, pers. obs.). Approximately 200 g of lean meat (usually Impala *Aepyceros melampus*) was deposited daily, either on the nest platform or in a favoured perch tree using the extendible mirror poles. Feeding continued until about 7 days after the first egg (allowing the birds time to lay a second) or until the eagles were obviously not going to breed. The target pairs were seen consuming the food directly, and three birds trapped shortly after supplementation averaged 30% heavier than other birds of their sex (see Simmons 1991 for sex-related mass differences). I predicted that increased food would: (i) enhance the likelihood that the pair would breed (on average only 64% of pairs breed in any one year; see above); (ii) induce earlier laying; (iii) increase clutch-size from one to two eggs (98% of all breeders naturally lay one-egg clutches: R.E. Simmons, unpubl. data) and (iv) increase egg size.

The mass of live eggs decreases uniformly throughout incubation, so density can be used to calculate laying and hatching dates, provided several eggs of known age are monitored throughout this period (Furness & Furness 1981). I did so for three known-age eggs and could thus backdate to within about ±5 days the laying dates of all breeding attempts (R.E. Simmons, unpubl.). Laying dates of food-supplemented pairs could then be compared with their own

laying dates in other years. Since laying periods differed slightly between years, dates were standardized by calculating the mean laying date for all birds in that year and computing each pair's laying date relative to the mean.

Definitions

Egg-laying (and not copulation) constituted a breeding attempt. Wahlberg's Eagles rear only one brood per year (Tarboton 1977, Steyn 1982, this study). The proportion of pairs breeding was defined as the number of pairs attempting to breed divided by the total number of territorial pairs present. The non-breeding portion comprises roughly 12–35% of all territorial pairs in most populations (Table 1). Breeding success for each population was taken as the mean number of young reared per breeding pair per annum, and population density was defined as the total number of breeding + non-breeding pairs per 100 km². Significance was set at P < 0.05 for all statistical tests.

RESULTS

Factors affecting the proportion of pairs breeding

In any one year, it is rare for all members of a population of African eagles to breed (e.g. Brown 1955, Steyn 1982,

Table 2. *Simple linear regression analyses of the proportion of Wahlberg's Eagle pairs breeding annually and their success (young/pair/year) in relation to five independent variables. The R² values indicate the variance explained by each variable alone. Data for the proportion of pairs breeding were extracted from five studies and those for breeding success from eight studies given in Table 1*

Independent variable	Proportion of pairs breeding R^2	Proportion of pairs breeding P	Breeding success R^2	Breeding success P
Density (pairs/100 km²)	82.4%	<0.01	85.60%[1]	<0.001
Latitude	15.0%	0.45	16.36%	0.32
Altitude	21.6%	0.35	6.73%	0.54
Rainfall (mm)	1.8%	0.80	2.44%	0.71
Years studied	21.5%	0.35	6.72%	0.55

[1] See Figure 1 for curvilinear relationship.

Gargett 1990). Wahlberg's Eagles are no exception: the proportion of pairs breeding in different populations throughout Africa varied from 64% to 88% (Table 1). Only population density was significantly correlated (P < 0.01) with the proportion of pairs breeding. Fewer pairs bred at high population densities in the six studies reporting this variable in south-central Africa (Table 2).

In the linear regression examination of variables influencing the proportion of pairs breeding (Table 2), both latitude and altitude explained some variation. However, using partial correlation with density held constant, altitude explained only 6% and latitude 24% of the variation. Hence, population density was the principal factor governing breeding frequency.

Density-dependent, latitudinal and altitudinal effects on breeding success

Population density also had pronounced significant (P < 0.001) effects on reproduction. In low-density areas (1–2 pairs/100 km²), productivity was twice as high (0.78 v 0.31 young/pair/year) as that in high-density areas (23 pairs/100 km²). Population density alone explained 94% of the variance in mean reproductive output of eight African Wahlberg's Eagle populations (Fig. 1).

Partial (linear) correlation procedures confirmed that nesting density was the principal determinant of breeding productivity: with latitude held constant, nest density remained highly correlated with breeding success ($R^2 = 76\%$, $n = 8$, P < 0.05). Latitude, however, explained only 7% of the variation ($n = 8$, n.s.) with density held constant.

No significant latitudinal effects on the number of young reared per breeding pair per year were evident in the eight studies reviewed (Tables 1 and 2). Altitudinal effects, suggested by some (e.g. Slagsvold 1981, Krementz & Handford 1984) to influence clutch-size in passerine birds, likewise played no role ($R^2 = 8.0\%$, $n = 5$, n.s.) in eagle reproductive success.

Rainfall effects on breeding success and proportion of pairs breeding

Mean annual rainfall, a variable known to have a negative influence on breeding frequency and productivity in some eagle populations (e.g. Gargett 1990), played no role in explaining productivity in Wahlberg's Eagle populations continent-wide ($R^2 = 1.4\%$, $n = 8$, n.s.). However, within the Sabi Sand population it had some effect. Comparing years (Table 3), higher "late" rains led to increased productivity ($r = 0.82$, $n = 4$, n.s.). This trend, however, also appeared density-related: density combined with rainfall in stepwise regression explained (R^2) 98% of the variation in young reared in different years. Within-population variation in productivity thus reflected the density-sensitive Africa-wide vari-
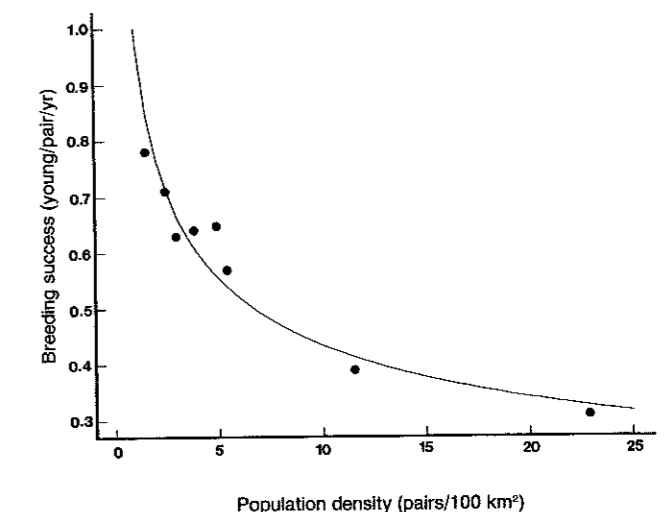

Figure 1. The significant (P < 0.001) decline in breeding success (young reared/breeding pair/year) with increasing population density of Wahlberg's Eagles throughout Africa. The number of young reared (Y) is described by the equation $Y = -0.028(\text{density})^{-0.35}$; $R^2 = 94\%$.

Table 3. *Population density and breeding of Wahlberg's Eagles in relation to rainfall in the Sabi Sand Reserve*

Year	Total pairs[1]	Breeding pairs No.	Breeding pairs %	Population density (pairs/ 100 km²)	Rainfall[2] (mm) Early	Rainfall[2] (mm) Late	Success[3]
1988	40	32	80%	21.2	18	71	0.13
1989	33	23	70%	22.2	3	67	0.48
1990	34	16	47%	22.9	27	65	0.47
1991	28	17	61%	19.5	6	24	0.29
Total	135	88	65%				0.31

[1] Total pairs differ after 1988 because the study area decreased in size then, not because fewer pairs bred.
[2] Early rains: August–September, when pairs begin breeding; late rains: October–December, brood rearing period.
[3] Number of young reared per breeding pair per year.

ation, although 4 years' data are insufficient for more sophisticated analyses.

Density-sensitive clutch-sizes

Continent-wide trends in the incidence of two-egg clutches support the idea of density-sensitive breeding, even though two eggs are uncommon. The incidence of two-egg clutches was significantly higher ($\chi^2_1 = 5.92$, $P < 0.01$) in the lower-density populations present in equatorial regions (1.5–3 nests/

Table 4. *The incidence of two-egg clutches (c/2) of Wahlberg's Eagles in different populations in Africa. Population density figures are given in Table 1 for all areas except Malawi (no data). Significant differences occurred between areas of differing density*

Area	All clutches	c/2 (%)
Equatorial		
East Africa[1] (0°–6°S)	31	3 (9.6%)
Malawi[2] (13°S)	6	1 (16.6%)
Subtropical		
Zimbabwe[3] (20°S)	724	18 (2.5%)
South Africa[4] (22.5°S)	142	7 (4.9%)
South Africa[5] (22.5°S)	88	2 (2.3%)

Sources: [1] East African nest record scheme (L. Bennun) and Delaware Museum nest records (D. Loubser); [2] Delaware Museum; [3] Zimbabwe nest record scheme (K. Hustler); [4] Tarboton & Allan (1984); [5] This study.

100 km²: Brown 1955, Smeenk 1974, Vande Weghe 1979) than in the high-density populations which exist in subtropical Africa (5.4–23 nests/100 km²; Snelling 1969, Steyn 1982, Tarboton & Allan 1984, this study). The approximately 5.5-fold lower density (2.4 v 13.3 pairs/100 km²) apparent between these groups was associated with a 3.9-fold increase (10.8% v 2.8%) in the number of two-egg clutches (Table 4).

Because these trends also reflected latitudinal differences (equatorial populations exhibited more two-egg clutches than subtropical populations), I checked this by correlating latitude of five areas (Kenya/Uganda, Malawi, Zimbabwe, northern South Africa, eastern South Africa: Table 4) with the incidence of two-egg clutches. No significant latitudinal trend was evident ($r = -0.62$, $n = 5$, n.s.).

Within-population comparisons

Strong support that continent-wide trends were density-sensitive was provided by the increasing incidence of two eggs in a declining population studied by W.R. Tarboton (*in litt.*). He monitored a 1.7-fold decline in population density over 10 years, from 6.3 pairs per 100 km² in 1975 to 3.7 pairs per 100 km² in 1984. The incidence of two-egg clutches rose from 1.4% (1 in 70 clutches) to 12.9% (4 in 31 clutches) in the same period. These proportions are significantly different when grouped for high- v low-density years (Fisher's exact test, $P = 0.03$). Thus, low-density populations exhibit more second eggs than high-density populations both within and between populations.

Effects of supplementary feeding

Of eight pairs given supplementary food in 1988 and 1989, only six bred (75%). This proportion is identical to the mean proportion of unsupplemented pairs that bred in 1988–1989 (Table 5).

Extra food also had no discernable effect on clutch size: no birds laid extra eggs as predicted. Of the six supplemented pairs that bred, all laid single eggs, despite being fed for at least 1 week after laying. Similarly, egg volumes of fed females did not differ significantly from those of their own eggs laid in non-supplemented years (Table 5). Another way of

Table 5. *Summary of the effects of supplementary food on the proportion of pairs breeding, clutch-size and egg size in a high-density population of Wahlberg's Eagles. Experiments took place in 1988 and 1989 and controls are taken only from those years. All differences were non-significant*

	Fed (n)		Unfed (n)	
Proportion of pairs breeding	75%	(8)	75.7%	(74)
Mean clutch-size	1.0	(6)	1.0	(56)
Mean egg volume (cc)	76.79	(5)	76.13	(5)[1]

[1] Controls were all other eggs laid by the same female in other years.

Table 6. *Laying dates of fed and unfed female Wahlberg's Eagles (in days) relative to the mean laying date of all birds for the year. + = after mean, − = before mean. Each comparison represents one (marked) female, while unfed controls may be the average of up to three other layings (variation given in brackets). Matched pair t-test, t = 0.42, n.s.*

	Laying date relative to mean for population					
Fed	+1	+5	−13	−2	+1	−2
Unfed	−11	+3	−11	−1	+19	+1
(range)	(−2, +6, −15)	(+9, −6)	(−11, −11, −11)			(+5, −4)
Fed bird laid earlier?	No	No	Yes	Yes	Yes	Yes

assessing the effect of food supplements is to determine how many times eggs from supplemented females were larger than in unsupplemented years. Of five eggs for which this was possible (one was taken prior to measurement), "fed" eggs were larger in only two cases and smaller in three cases. Again, extra food appeared to have no consistent effect (matched pair *t*-test, $t = 0.33$, n.s.).

In other supplementation studies (reviews in Ewald & Rowher 1982, Arcese & Smith 1988, Simmons 1989), clutch-size increases were less common than earlier laying dates. However, extra food also had no discernable effect on laying dates among Wahlberg's Eagles. Laying dates of supplemented females, compared with their laying dates in other years (and adjusted to the mean of the year in which eggs were laid), were earlier in four cases (mean 6 days earlier) and later in two other cases (mean 3 days later). Matched pair *t*-tests showed no significant differences (Table 6). Supplementary food thus had no effect on any of those reproductive variables which are typically influenced in other species.

Factors affecting population density

Food resources are usually thought to influence population density of breeding raptors unless factors such as a paucity of nest sites sets a limit lower than the carrying capacity (Newton 1979). I correlated latitude, altitude and mean annual rainfall with population density for the eight eagle studies (Table 1) to determine if these factors influenced population density. No significant correlations were apparent (Table 7).

DISCUSSION

Density-sensitive breeding effects have been demonstrated in a variety of smaller species (Klomp 1970, Dhondt *et al.* 1992), and high densities in these species significantly affected growth and survival of young and, less consistently, egg sizes or clutch-sizes (Arcese & Smith 1988, Torok & Toth 1988, Sinclair 1989). Efforts to find density effects in larger species have generally failed (Newton 1986, Donázar 1990, Gargett 1990), although reduced breeding success was found in dense populations of African Fish Eagles *Haliaetus vocifer* (Thiollay & Meyer 1978) and some populations of Golden

Eagles *Aquila chrysaetos* (Haller 1982, Thompson *et al.* 1982). However, few studies have found continent-wide, density-dependent breeding as documented here for Wahlberg's Eagles; such trends have rarely been verified within populations and even less often experimentally tested.

Since rainfall is strongly related to primary productivity (Rosenzweig 1968, Deshmukh 1986) and has been used to deduce food resource variations with clutch-size (Ricklefs 1980), it is not unreasonable to use mean annual rainfall as an index for food resources for predatory birds. Particularly in subtropical areas, timing of breeding of raptors (Steyn 1982, Simmons 1989, Kemp 1991) and the abundance and survival of their avian (Earlé 1981a,b, Maclean 1990, Peach *et al.* 1991) and mammalian prey (Delany 1972, Taylor & Green 1976) are positively influenced by rainfall. Hence, precipitation should be an appropriate measure of food resources for eagles which eat small mammals and nestling birds (Tarboton 1977, Steyn 1982, Simmons 1992). However, neither rainfall nor latitude played any role in explaining variations in the proportion of pairs breeding annually or their success in south-central Africa. The low and non-significant correlations with rainfall thus suggest that food resources play little direct role in reproductive variations. Unlike other studies, I checked these trends by examining within-population variation and then providing extra food to pairs within dense populations. Each result confirmed the initial impressions: variation in Wahlberg's Eagle breeding is strongly related to population density but not to food resources.

A widely accepted idea is that population density itself is ultimately influenced by food resources (Lack 1954, Newton 1979, Martin 1987), and thus, indirectly, density-reduced reproduction occurs because of lower resource levels per

Table 7. *Simple linear regression analyses of population density in relation to latitude, altitude and mean annual rainfall for eight studies of Wahlberg's Eagles in Africa*

Independent variable	R^2	P
Latitude	13.35%	0.37
Altitude	15.05%	0.34
Rainfall	3.14%	0.67

individual. Only one experimental study has previously checked this supposition and confirmed that individuals in high-density populations show reduced productivity because of low food resources (Arcese & Smith 1988). The supposition was not supported for food-supplemented Wahlberg's Eagles. This occurred despite the increased condition and body-mass of the experimental pairs; the result is thus unique and suggests that pairs may be witholding reproductive effort. That is, pairs may be adaptively refraining from breeding (in the sense of Curio 1983) for lifetime benefits, rather than being constrained by reduced food resources. However, before we can accept such a conclusion, I explore alternative (constraint) explanations.

In some experimental studies, Smith et al. (1980) and Ewald & Rowher (1982) have suggested that food quality was inappropriate and led to false negative responses. Since the supplemented red meat was little different in quality from the protein normally consumed by these eagles (Tarboton 1977, Steyn 1982), food type cannot be considered a confounding variable. Food quantity was probably adequate also since the total daily supplement of 200 g of meat during laying represents a very high biomass: unpublished observations show that the biomass naturally provisioned by these birds is c. 150 g per day. Indeed all retrapped birds which were supplemented had on average increased by 30% in body-mass.

Several other factors may explain these unusual results: first, they may be a statistical artifact of the low variation in clutch-and brood-size of these eagles. This seems unlikely because relatively large samples from populations across the species' range were available for geographic analyses, although experimental nests were admittedly limited. Moreover, the inference from three different levels of analysis (Africa-wide, within-population and experimental) all led to consistently similar conclusions. Second, the lack of response to food supplements in my study area may have occurred because of the low sample sizes (limited because of the time needed to provide meat to well-dispersed birds) and type II statistical errors. If this is so, then further supplements would resolve the problem. Again this seems unlikely because other analyses implicating food (e.g. rainfall) also suggested that food resources were unimportant in explaining breeding. Third, clutch-size (hence brood-size) may be a genetically fixed trait which may not respond to environmental variation. This too is falsified by the declining incidence of two-egg clutches in the densest populations in south-central Africa and the increasing proportion of two-egg clutches in Tarboton's declining population. Since clutches in the latter area were laid by pairs that had previously laid single eggs, changes in age structure or individuals cannot explain the results. Thus clutch-size is ecologically sensitive. Fourth, low reproductive success in dense populations cannot be attributed merely to the increased occurrence of non-breeding pairs: the success of *breeding* females also declined (Fig. 1) in dense populations, falsifying this idea.

A final possibility is that extrinsic factors covary with dense eagle populations to limit reproductive success. This is pos-sible since other predators breed in areas attractive to Wahlberg's Eagles (high densities of other raptors were evident in the study area: Simmons 1992). However, such species (Hawk Eagle *Hieraaetus spilogaster* and Tawny Eagle *Aquila rapax*) are both larger and feed on different types and sizes of prey (Steyn 1982). Both species have also largely finished breeding when Wahlberg's Eagles start (R.E. Simmons, unpubl. data). This would minimize any indirect interspecific food competition likely to affect breeding.

In conclusion, the observed variation in breeding of Wahlberg's Eagles was more closely tied with population density than with correlates of food supply (rainfall). Food supplements to check the idea that food resources are reduced for individuals in dense populations suggested that this was not the case.

Adaptive restraint v constraint explanations

Most density-dependent explanations of reduced reproduction in birds implicitly assume that smaller clutches, broods and overall success arise from ecological constraints in the form of decreased food resources for individuals or decreased access to those resources (Lack 1954, Newton 1979, Arcese & Smith 1988, but see O'Connor 1982, Dhondt et al. 1992). Since food was not limiting to the experimental eagle pairs, we must look instead for adaptive explanations for reduced reproduction in dense populations.

One such life-history explanation of these results is that lifetime benefits override any immediate advantages: long-lived species existing in dense (saturated) populations may benefit by skipping breeding and then rearing high-quality young when they do breed. If high-quality young are particularly important in saturated environments in which they have a low probability of survival or gaining breeding places (Simmons 1988), then one would expect adults to miss breeding opportunities in an effort to avoid jeopardizing future reproductive abilities (Williams 1966, Curio 1983). This might have two benefits: adults that skip breeding may live longer and thereby enjoy greater lifetime success (Newton 1989), or larger eggs and heavier, higher-quality young may result from greater investment following a nonbreeding year. Evidence for such reproductive "restraint" was suggested in this population by a significantly greater proportion of adults skipping breeding one year after attempts to rear two young (R.E. Simmons, unpubl.). This also occurs in other species (Reznick 1985, Roskaft 1985, Partridge 1989). If this breeding gap was due to food constraint and a loss of body condition, one would expect to see increased mortality one year later. This was not so (R.E. Simmons, unpubl.), hence a more likely explanation is adaptive restraint. Such "restraint" could evolve if either adults ultimately left more recruitable offspring in their lifetime or their reproductive lifespan itself was increased. Skipping breeding for these reasons has also been suggested for long-lived shearwaters (Wooller et al. 1989). Most recent emphasis has been put on the number of young produced in a lifetime (Newton 1989) rather than the quality of the young produced. I believe (Simmons 1988) that, for the longer-lived species, offspring

quality has been erroneously neglected in assessments of lifetime fitness.

The more frequent occurrence of two eggs in the least dense populations suggests that pairs may be favouring the rearing of two poorer-quality young where future breeding possibilities are less restricted than in saturated populations. (In dense populations such as the one studied, only four spaces in 40 territories were "available" for new breeders of each sex per year [Simmons 1993].) The only known case of Wahlberg's Eagles rearing two young was in a low-density population on the very edge of the range in eastern South Africa (J. Mendelsohn, pers. comm.). Tawny Eagles also rear two young more often in low-density populations where (contrary to expectation) primary productivity is lower (Hustler & Howells 1989). Hence if adults are tuned to assess not only their immediate reproductive benefits but also the future likelihood of their young breeding, then density-sensitive inhibition (a very simple proximate mechanism) unrelated to food supplies could evolve. I suggest it has done so in Wahlberg's Eagles.

Other food supplementation experiments also suggest adaptive restraint rather than mere food constraint. For example, Meijer et al. (1988) food supplemented late-laying Kestrels *Falco tinnunculus* and found that, contrary to breeding being food limited, experimental birds did not lay significantly larger clutches than control pairs. Early-laying birds, however, did respond. Similar results were apparent but not emphasized in Arcese & Smith's (1988) passerine study. Both studies suggested that late-laying females, despite substantial food resources, limit their clutch- and brood-size probably because large late broods have little chance of success; future fitness components of the breeders are thus maximized (Daan et al. 1990). Such intriguing results demand further experimental studies of apparently food-limited breeding to tease apart adaptive restraint from ecological constraint.

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