

Can the Common Kestrel *Falco tinnunculus* provision Increased Broods in a mid-latitude environment?

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ABSTRACT

Brood manipulations have traditionally been used to test Lack's hypothesis (1954) that birds lay a clutch size that maximizes the number of offspring they fledge. Results of manipulations vary from those that show parents are unable to raise experimentally enlarged broods to those where parents successfully raise extra nestlings without obvious detrimental effects. I reviewed the literature on brood manipulations to evaluate whether latitudinal differences between study areas partly explain the variation in experimental results. Three previous brood manipulations at mid-latitudes (24° - 45°) demonstrated that parents were unable to provide sufficient food to their offspring. To test whether other species are unable to raise enlarged broods in mid-latitudes, I manipulated Common Kestrel broods in the Western Cape Province, South Africa (34°S) and monitored provisioning rate, nest attendance and nestling growth and survival. Parents of enlarged broods (+2) were able to increase their provisioning rates to such an extent that their nestlings obtained as much food as control broods. While females of enlarged broods did not make any increased effort to hunt around the nest site while attending the brood, there was a decrease in the amount of food caching in the enlarged broods, suggesting that they were probably being provisioned at close to their maximum rate. The results of this study do not support the hypothesis that birds are constrained by food during reproduction at mid-latitudes.

INTRODUCTION

Clutch size is regarded as a major trait in life-history evolution (Stearns 1992) and is one of the easiest parameters to measure. Lack (1954; 1966) hypothesized that birds should lay a clutch size which maximizes their number of offspring. In a proximate sense, this means that they create a brood size which they can adequately nourish. Several other clutch size hypotheses have been proposed relating to seasonality of resources and resultant population levels (Ashmole 1963; Ricklefs 1980), habitat use (O'Connor 1982), adaptive lifetime response (Williams 1966; Klomp 1970) and energy allocation (Cody 1966; 1971). Brood manipulations are an easy experimental method of testing Lack's ideas and in the last four decades, broods of many species have been manipulated (51 studies reviewed by Dijkstra *et al.* 1990; Dann 1988; Navarro 1991; Beissinger 1990; Gard & Bird 1992;

Robinson & Rotenberry 1991; Kallander & Smith 1990; Husby 1986; Sanz 1997). Some studies have supported Lack's hypothesis, but many found that birds were able to raise more chicks than the average clutch size (Gustafsson & Sutherland 1988; Pettifor *et al.* 1988; Hegner & Wingfield 1987). The cost of reproduction to parents was used as a possible explanation for these discrepancies (Reznick 1985; Nur 1988a) and studies subsequently addressed the issues of future reproduction of parents following experimental manipulation as well as the survival of offspring after fledging (Dijkstra *et al.* 1990).

Obtaining data on lifetime reproductive success is difficult and few brood manipulation studies have been published during the 1990s. The results of studies that address the issues of reproductive costs are divided amongst those showing definite reproductive costs when raising more chicks than determined by clutch size (Roskaft 1985; Hegner & Wingfield 1987; Dijkstra *et al.* 1990) and those showing no effect on the parents (Korpimäki 1988). Monaghan and Nager (1997) point out that most brood manipulations do not take into account the costs of laying and incubation and are restricted to one part of the breeding phase, namely chick-rearing. They suggest that by including all components of the breeding phase in the manipulation, increased broods may show an effect on the cost of reproduction. Reznick (1992) goes further and argues that experimental manipulations are not good indicators of reproductive costs and that costs can better be determined by quantitative genetics.

Most brood manipulations have been conducted in high latitude regions (48° - 76° latitude) where clutch sizes are generally larger than in mid- (29° - 42° latitude) and tropical (0° - 18° latitude) regions (Klomp 1970; Husell 1985). The breeding season is short in high latitude regions and some raptor prey populations such as voles are known to show large year-to-year variations in numbers (Hansson & Henttonen 1985; Korpimäki & Rita 1996). Food supply has been postulated as a reason for the differences in clutch size between low and high latitude regions in raptors (Simmons 1989a; Beissinger 1990). I hypothesize that birds at high latitudes are, on average, able to cater for the increased number of chicks in manipulations because of the high food availability during peaks in these large prey population fluctuations. Assuming that these birds allow for a greater food resource margin than those at mid- and low latitudes because of a higher variation in food availability, these birds would have more food available to raise increased broods. In brood manipulations at mid- and low latitudes, parents in three species were unable to increase provisioning rates to provide sufficient food for the enlarged broods (Simmons 1986; 1989a; 1997).

I manipulated the broods of Common Kestrel in a mid-latitude environment where prey populations appear to have smaller year-to-year fluctuations than those in high latitudes (Hansson & Henttonen 1985). The aim of the manipulation was to test whether kestrels were able to provide sufficient food to chicks in a mid-latitude environment when having to feed broods larger than the maximum number determined by clutch size.

STUDY AREA

The study was conducted in the Western Cape Province, South Africa (34°S, 18°E) at sites between the Cape Peninsula and Langebaan, 130 km to the north. The area includes the city of Cape Town roughly in the central western section of the study area. The topography varies from quartzitic sandstone mountains on the Cape Peninsula (including Table Mountain) to siliceous and calcareous sandy flats north to Langebaan. The area experiences a Mediterranean-type climate characterized by cool, wet winters and warm, dry summers. Rainfall is highly variable depending on the exact location. On the Cape Peninsula it varies from 400 mm per annum in the southern Peninsula to 2270 mm per annum on Table Mountain. The flat, low-lying areas north of Cape Town have an annual rainfall of 500-600 mm per annum (Cowling *et al.* 1996). Temperatures are relatively constant and mild, with mean annual values ranging between 16°C and 22°C and with a range of mean minimum and maximum temperatures of 6°C and 10°C. The study area experiences strong winds from the northwest during the winter ranging from 20-30 km per hour. During summer, southeast winds blow at speeds of 20-40 km per hour.

Kestrel pairs were scattered over the whole area including urban habitats, mountain slopes and

open scrub. Nests were found on the cliffs of the mountains on the Peninsula, on buildings in urban or suburban areas and in quarries when no natural nesting sites were available.

METHODS

Brood manipulations were conducted between October and December 1994: brood size was increased in 4 nests and reduced in 5 nests. Five additional nests were used as controls. Manipulations were randomly allocated to nests of different laying dates, clutch sizes and habitats (Table 1). Hatching dates were determined by checking the nests regularly and inspecting the eggs for pipping. Some nests were not checked on the day the eggs hatched and the hatching date for these broods were determined by backdating after estimating the age of the nestlings. Estimations were done within the first two weeks after hatching and the age of nestlings was estimated by comparing size and down-plumage changes with photographs taken of chicks of known ages (Van Zyl 1993). Because nestlings hatched on different days with a maximum of 5 days between the first and last hatching (Van Zyl in press), the estimated date of hatching of the oldest nestling was used in the calculations of nestling age for the brood. Broods were manipulated by adding two more chicks than the original clutch size to increase the brood size or by subtracting two chicks from the original clutch size (Dijkstra *et al.* 1990). Controls were not manipulated unless all the eggs did not hatch, in which case nestlings were added so that the brood size equalled the clutch size. An extra chick had to be provided to two control broods because of nestling fatality soon after hatching. Ages of introduced chicks did not differ by more than three days from the study brood ($x = 0.7$ days, range 0 - 3 days, $n = 7$) and introductions were made when chicks were between 3 and 16 days old ($x = 9.3$ days, $n = 7$).

Food delivered to the nestlings was monitored by full day watches at the nest. During these watches, nest attendance by parents was scored to the minute. The nest site was observed from a concealed position 40 - 100 m from the nest and all food brought to the nest was identified where possible. When prey items were clearly seen, they were rated according to size by estimating the length of the item in centimeters relative to tarsus length for small items and to tail length for large items. The prey items were placed into three size categories for analysis based on their estimated body length (Table 2). It was impossible to determine if nestlings ate all food provided to them but it was assumed that all items delivered to the nest were consumed by the nestlings. However, especially when chicks were young, food was sometimes left on the nest and later eaten by the adults. It was also impossible to determine the exact mass of the food provisioned. Thus, data were initially analysed using two prey mass estimates. Prey mass was estimated for all the size categories (Table 2) in the first analysis and the total mass of prey delivered to the observed nests totalled 3386.8 grams. In the second analysis, published estimates based on consumption times of average invertebrate (0.6 grams) and average vertebrate (12.8 grams) prey items were used (Van Zyl 1994) and the total mass of prey delivered to the nests totalled 3685.4 grams. This calculation is less than 9% more than the analysis based on estimated prey sizes. Findings from the two analyses were found not to be statistically different (Mann Whitney U-test, $p=0.81$). For comparison in this study, all calculations of prey mass were performed using the two published estimates for kestrel vertebrate and invertebrate prey (Van Zyl 1994). Using these generalized masses can be justified because of errors inherent in estimating prey size and hence prey mass. Prey brought to the nest is often plucked and partly eaten so prey mass is overestimated, while on the other hand, nestlings do not necessarily eat all prey provided. This procedure also provides comparable results to a study of Common Kestrels in the Eastern Cape Province, South Africa where similarly-sized prey were provisioned (Van Zyl in press).

Provisioning rates have been correlated to the hunger calls of the brood (Bengtsson & Ryden 1983; Masman *et al.* 1989). Screaming intensities of nestlings were not explicitly recorded in this study but no excessive screaming was heard.

Nestling mass and wing length were measured at various ages and were used as indices of nestling growth. However, measurements were taken only once or twice during the development of the nestlings which allowed a very limited comparison of growth. Nestling survival was equated to the number of nestlings surviving beyond 25 days: most nestlings surviving to this age fledge successfully (Van Zyl 1993).

Two or three days of observations were conducted during the nestling cycle at each nest to avoid biases by days of unusually high or low provisioning rates (Simmons 1989b). These observations were then averaged to avoid pseudoreplication (*sensu* Hurlbert 1984). However, while all statistical tests and differences between groups use these averaged data, figures also include the raw data points for each observation day to indicate the range of the data. To allow comparison of provisioning rates and nest attendance scores for nestlings of different ages, provisioning rates and nest attendance were adjusted for nestling mass. Nestling mass was estimated from sigmoid growth curves plotted from nestling measurements ($r^2 = 0.979$, $n = 19$) using the formula:

$$\text{estimated chick mass} = 228.428 / (1 + \exp(-(age - 8.482) / 3.753))$$

Kruskal-Wallis one-way analysis of variance and Mann Whitney U-tests were used in data analyses from the statistical software packages StatGraphics version 4.0 (STSC 1984) and Statistix for Windows version 1.0 (Analytical Software 1996).

Table 1. Information on breeding sites of Rock Kestrels used in the brood manipulation experiment

Nest Site	Exp	Eggs	Hatched	Add/ Remove	Est. Hatch Date	Manip. Date	Nest Site	Habitat
Rondeberg Quarry Upper east	Red.	4	3	-2+1	9 October	13 October	Quarry	Scrub
Tafelsig/Seesig	Enlarg.	4	4	+2	10 October	13 October	Building	Suburbia
Rondeberg Quarry Lower west	Contr.	4	3	+1	19 October	27 October	Quarry	Scrub
Tygerberg Quarry	Red.	4	4	-2	22 October	3 November	Quarry	Scrub/suburbia
Dorsberg Upper section	Enlarg.	5	5	+2	22 October	3 November	Quarry	Scrub
Escom Nestbox	Contr.	4	4	0	26 October	-	Building	Suburbia
Durbanville Quarry	Contr.	4	4	0	28 October	-	Quarry	Scrub/suburbia
Tygerberg Hospital	Contr.	4	4	0	4 November	-	Building	Suburbia
Rondeberg Quarry Lower Middle	Red.	4	4	-2	6 November	18 November	Quarry	Scrub
Kommetjie	Enlarg.	4	4	+2	6 November	18 November	Cliff	Scrub
Devil's Peak	Red.	3	2	-1	9 November	28 November	Cliff	Scrub
Lion's Head - South	Contr.	4	3	+1	12 November	28 November	Cliff	Scrub
*Scarborough	Red.	4	4	-2	6 November	16 November	Cliff	Scrub
**Dorsberg Quarry North	Enlarg.	3	3	+2	6 November	18 November	Quarry	Scrub

* Nestlings disappeared within 10 days of manipulation. Possibly predated by baboons.

** Nestlings killed by a snake 14 days after manipulation.

Table 2. Provisioning and estimated sizes and masses of prey fed to enlarged, control and reduced broods. Number of prey items per prey type and size are in the order of enlarged/control/reduced broods.

Vertebrates:

Mammalia	<i>Small</i> (<4cm; 6g)	<i>Medium</i> (4-6cm; 15g)	<i>Large</i> (>6cm; 22g)
<i>Rhodomys pumilio</i>	0/0/0	1/1/2	0/0/3
Unidentified moles	0/0/0	0/0/1	0/0/0
Unidentified rodents or shrews	4/1/1	3/5/4	1/1/1
Total prey items	4/1/1	4/6/7	1/1/4
Reptilia	<i>Small</i> (<4cm; 4g)	<i>Medium</i> (4-12cm; 8g)	<i>Large</i> (>12cm; 15g)
<i>Agama</i> spp	0/0/0	1/0/0	0/0/0
<i>Bradypodion occidentale</i>	0/0/0	11/1/1	0/0/0
<i>Cordylus</i> spp	0/0/0	0/0/3	0/0/0
Unidentified geckos	0/0/0	0/0/1	0/0/0
Unidentified lizards	1/0/0	41/11/14	4/1/8
<i>Meroles</i> spp	0/0/0	0/4/1	0/4/4
<i>Nucras</i> spp	0/0/0	0/0/0	0/0/1
<i>Mabuya</i> spp	1/0/0	6/2/2	4/3/8
Unidentified snakes	0/0/0	0/2/0	0/1/1
Total prey items	2/0/0	59/20/22	8/9/22
Aves	<i>Small</i> (<4cm; 8g)	<i>Medium</i> (4-5cm; 15g)	<i>Large</i> (>5cm; 25g)
Unidentified birds	13/5/3	25/18/6	1/0/0
<i>Passer melanurus</i>	0/0/0	1/1/1	0/0/0
<i>Cisticola</i> spp	1/0/0	0/0/0	0/0/0
<i>Numida meleagris</i> day-olds	0/0/0	1/0/0	1/0/0
<i>Streptopelia</i> spp	0/0/0	0/0/0	0/1/0
<i>Streptopelia senegalensis</i>	0/0/0	0/0/0	1/0/0
<i>Passer</i> spp	0/2/0	4/4/2	1/0/0
<i>Sturnus vulgaris</i>	0/0/0	0/0/0	1/2/0
<i>Parus afer</i>	0/0/0	1/0/0	0/0/0
<i>Motacilla capensis</i>	0/0/0	0/2/0	0/0/0
Total prey items	14/7/3	32/25/9	5/3/0
Unidentified vertebrates	<i>Small</i> (<4cm; 6g)	<i>Medium</i> (4-6cm; 8g)	<i>Large</i> (>6cm; 15g)
	4/7/1	0/0/0	1/0/0
Invertebrates	<i>Small</i> (<3cm; 0.6g)	<i>Medium</i> (3-4cm; 1g)	<i>Large</i> (>4cm; 3g)
<i>Solifugidae</i> spp	3/1/0	1/1/0	0/0/0
<i>Orthoptera</i> spp	4/0/0	3/1/3	0/0/2
<i>Arachnidae</i> spp	1/0/0	0/0/0	0/0/0
Unidentified invertebrates	19/8/12	7/1/10	0/0/1
Total prey items	27/9/12	11/3/13	0/0/3
Unknown	(size unknown; 1g)		
Total prey items	17/4/8		

RESULTS

Nest attendance

Nest attendance declined with age of the nestlings in both treatments and controls ($y = -1.49x + 109.7$, $r^2 = 0.32$, $n = 25$, excluding two outlier points at 15 and 20 days old, Fig. 1). Except for the low nest attendance by one pair over two observation days, there appeared to be a minimum nest attendance time depending on the age of the nestlings which could be represented by the following equation:

$$\% \text{ time at the nest site} = 113.27 - (2.64 * \text{nestling age}) \text{ (} r^2 = 0.99, n = 7 \text{)}$$

Figure 1: The relation of nest attendance of parent kestrels and age of nestlings for enlarged (□), control (Δ) and reduced (O) broods. The solid line (—) is the average regression of nest attendance per nestling age ($y = -1.49x + 109.7$, $r^2 = 0.32$, $n = 25$, excludes two outlier points at 15 and 20 days old). The dashed line (---) is the regression of the threshold for nest attendance and nestling age ($y = -2.64x + 113.27$, $r^2 = 0.99$, $n = 7$).

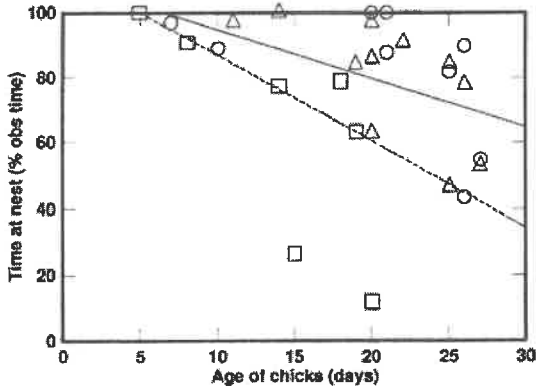


Figure 2: Nest attendance corrected for nestling age for enlarged (□), control (Δ) and reduced (O) broods. The individual points are age corrected nest attendance figures for each observation day, while the average and standard deviation for means for 2 or 3 observation days are shown as vertical bars.

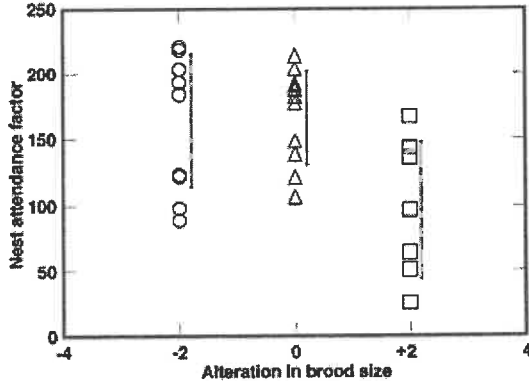


Figure 3: Nest attendance of males and females at various ages of the chicks for enlarged (□), control (Δ) and reduced (O) broods. Points connected are for males (solid) and females (open) of the same pair representing one day of observation.

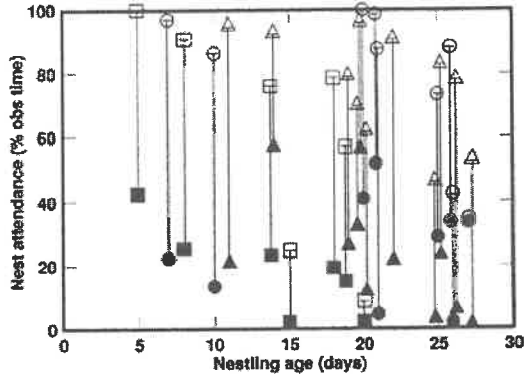


Figure 4: Parental contributions to the nestlings for enlarged ($\square$), control (Δ) and reduced (O) broods as number of items brought to the nest. Dotted lines (.....) indicate values for which the male contributes 75% of the items, where both male and female make equal contributions and for which the female contributes 75% of the items.

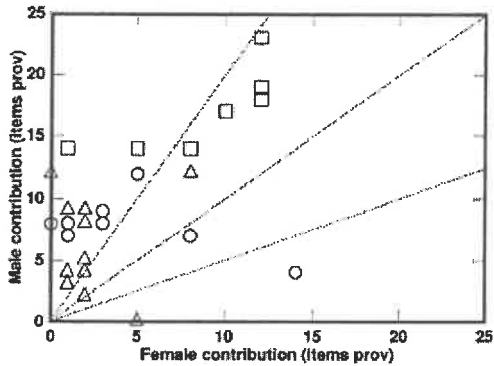
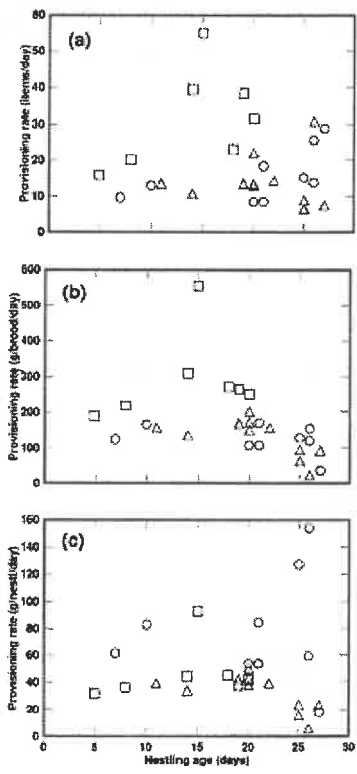


Figure 5: Provisioning rate to nestlings of different ages for enlarged ($\square$), control (Δ) and reduced (O) broods in units of (a) items per 14 hour day, (b) grams provisioned to the brood per 14 hour day and (c) grams provisioned per nestling per 14 hour day.

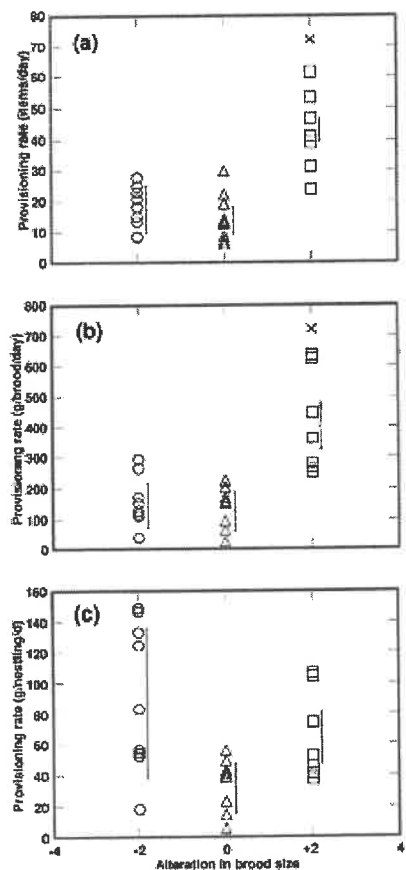


Nest attendance was lower in enlarged compared to control and reduced broods although this difference was not statistically significant (Kruskal-Wallis, $p=0.15$; Fig. 2). Females spent much more time at the nest than males (Paired t-test, $t = 10.23$, $n = 27$, $p<0.001$). The low nest attendance at the nest where attendance on two days was below the threshold attendance time was mostly due to the female who was away for similar periods to the male (Fig. 3).

Provisioning rate

Provisioning rate was measured as the number of food items delivered to the brood per day, estimated mass of food provided to the brood per day and estimated mass of food provided per nestling per day. Both male and female provided food to the nestlings, although the male provided most (Fig. 4). Provisioning rate increased with nestling age (Fig. 5a). There was a decrease in mass of prey delivered to control broods of 25 days old and older (Fig. 5b) and hence a decrease in mass of prey delivered per nestling (Fig. 5c). However, the mass of food provisioned to broods of 25 days old and older was not significantly lower than that provisioned to younger broods (Mann-Whitney U-test, $Z=1.01$, $p>0.05$). When provisioning rates were corrected for the age of the nestlings, parents of enlarged broods provided significantly more food in terms of items (Fig. 6a) and mass to the brood (Kruskal-Wallis, $p<0.05$; Fig. 6b) than did parents of controls and reduced broods. There was, however, no significant difference between treatments in the amount of food provisioned per nestling (Fig. 6c). Parents of reduced broods did not decrease the amount of food brought to the nest (Fig. 6b) resulting in more food per nestling in some reduced broods (Fig. 6c) than in control and enlarged broods. Parents of enlarged broods appeared to over-compensate for the extra nestlings and provided on average more food per nestling than parents of control broods (Fig. 6c).

Figure 6: Provisioning rates corrected for nestling age by standardizing rates for 218 gram nestling mass (20 days old) for enlarged ($\square$), control (Δ) and reduced ($\circ$) broods in units of (a) items per 14 hour day, (b) grams provisioned to the brood per 14 hour day and (c) grams provisioned per nestling per 14 hour day. The individual points are age corrected provisioning rates for each observation day while the average and standard deviations are shown as vertical bars. Asterisks indicate significant differences of $p<0.05$.



Prey species provisioned to the nest - proportion of vertebrates vs invertebrates

A variety of mammals, birds, reptiles and invertebrates ranging in size from Laughing Doves (*Streptopelia senegalensis*) to small grasshoppers was brought to the nest (Table 2). There was no difference in the number of prey items for each size category brought to the nest for the various animal taxa (Kruskal-Wallis, $p>0.05$). The majority of prey provisioned was vertebrate (Mann-Whitney U-test, $p<0.001$; Table 3). A slightly higher proportion of vertebrates was provisioned to the control and enlarged broods than to reduced broods, but this was not statistically significant (Kruskal-Wallis, $p>0.05$).

Table 3. Proportions of vertebrate and invertebrate prey delivered to the nests of enlarged (n=3), control (n=5) and reduced broods (n=4). Proportions are not significantly different from one another (Kruskal-Wallis, $p>0.05$).

NEST SITE	Vertebrates	Invertebrates	Unknown
<i>Enlarged:</i>			
Tafelsig/Seesig	51	4	2
Dorstberg Upper section	39	26	2
Kommetjie	46	6	13
TOTAL	136 (72%)	36 (19%)	17 (9%)
<i>Control:</i>			
Rondeberg Quarry Lower west	30	4	3
Escom Nestbox	21	0	0
Durbanville Quarry	15	2	0
Tygerberg Hospital	9	0	1
Lion's Head - South	3	6	0
TOTAL	78 (83%)	12 (13%)	4 (4%)
<i>Reduced:</i>			
Rondeberg Quarry Upper east	33	5	0
Tygerberg Quarry	16	0	0
Rondeberg Quarry Lower Middle	6	21	6
Devil's Peak	14	3	2
TOTAL	69 (65%)	29 (27%)	8 (8%)

Strike rates within 100 metres of the nest site

Females made significantly more strikes around the nest (<100m away) than males (2.28 vs. 0.71 strikes per 14 hour day respectively; Mann Whitney U-test, $p<0.005$). There was no difference in strike rates or strike success close to the nest for either sex between treatments and controls.

Caching

Prey was cached when chicks refused the food, when food had been recently provided to the brood or when the female refused food from the male. There was no significant variation in the delivery rate through the day for reduced, control and enlarged broods (ANOVA, $F=0.07$, $p=0.97$; $F=0.69$, $p=0.57$; $F=2.31$, $p=0.15$ respectively) suggesting that food was not cached because of irregular food supply through the day. There was no significant difference in the number of days that caching was observed or in the rate of caching by pairs with different brood sizes (Kruskal-Wallis, $p>0.05$). However, caching of prey brought to the nest site was performed more frequently for reduced (89%; 8 of 9 observation days) than control (36%; 4 of 11 observation days) and enlarged (43%; 3 of 7 observation days) broods. All pairs of the four reduced broods cached prey, while three of the five control pairs and only one of three pairs with enlarged broods cached prey. On average, reduced broods also had a higher caching rate (3.2 caches per day) than control and enlarged broods (1.3 and 1.0 caches per day respectively).

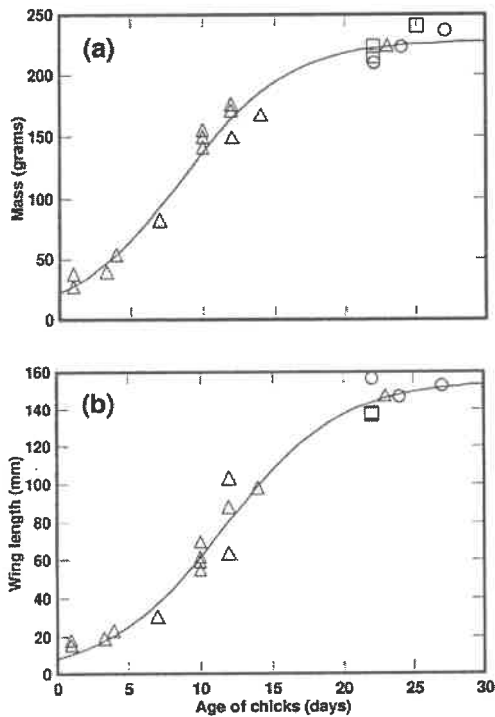
Provisioning rate and nest attendance

There was a negative correlation between provisioning rate and nest attendance for daily values for all the pairs combined (items provided per hour = $98.2 - (15.98 * \text{nest attendance})$; $p=0.002$; $r^2=31.75$; $n=27$). This suggests that parents sacrificed time spent attending the nest in order to hunt.

Nestling survival and growth

Sample sizes were too small to statistically analyse the effect of increased brood size on nestling survival and growth. However, there were no differences in either mass or wing lengths of similarly-aged nestlings in enlarged, control and reduced broods (Fig. 7). All nestlings of observed broods survived past 25 days old, although one fledgling was recovered dead below the nest of an enlarged brood soon after leaving the nest. All the nestlings of one enlarged brood were killed by a snake and one reduced brood disappeared between the manipulation and first observation day (Table 1).

Figure 7: Growth rates of nestlings of enlarged ($\square$), control (Δ) and reduced (O) broods using (a) nestling mass and (b) nestling wing length as indicators of growth.



Other brood manipulations

The majority of brood enlargements have shown that birds are able to raise more nestlings than determined by clutch size (reviewed in Dijkstra *et al.* 1990; Stearns 1992; Table 4). However, this has been demonstrated less conclusively at low and mid-latitudes, (10 of 17 studies, 59%) than at high latitudes (24 of 29 studies, 83%; $c^2=3.74$, $d.f.=1$, $p=0.052$; Table 4). Studies at low and mid-latitudes have more frequently demonstrated decreases in fledgling body mass (11 of 15 studies, 73%) and survival to fledging (11 of 16 studies, 69%) than have studies at high latitudes (10 of 20 studies, 50%, $c^2=6.07$, $d.f.=1$, $p=0.013$ and 13 of 25 studies, 52%, $c^2=7.32$, $d.f.=1$, $p=0.007$; Table 4). The influence of brood enlargements was lower at low and mid-latitudes than at high latitudes on the body mass (0% vs 83%), survival (0% vs 43%) and future reproductive performance of parents (25% vs 57%; Table 4).

Table 4. Results of brood manipulation experiments at low, mid- and high latitudes. Life-history details of offspring and parents are indicated as an increase (+), decrease (-) or no difference from controls (0). Fledge = number of offspring that left the nest; Survival -fledge = survival of nestlings until fledging; Survival-season = survival of fledglings until autumn or the next breeding season; Future breeding = future breeding performance of the parents

Species	Offspring Fledge	Body mass	Survival -fledge	Survival -season	Parents Body mass	Survival Future breeding	Latitude	Hemis- phere	Reference
Low latitudes (0° - 23° latitude)									
<i>Puffinus puffinus</i>	-	-	-		0		0	S	Harris (1969)
<i>Oceanodroma castro</i>	-	-	-				0	S	Harris (1969)
<i>Creagrurus furcatus</i>	+	0	0		0	0	0	S	Harris (1970)
<i>Sula sula</i>	-		-				8	S	Nelson (1966)
<i>Rostirhamus sociabilis</i>			-				10	N	Beissinger (1990)
<i>Quelea quelea</i>	0	0	-				10	N	Ward (1965)
<i>Aerodramus spodiopygius</i>	0	-	-				18	S	Tarburton (1987)
Mid-latitudes (24° - 45° latitude)									
<i>Accipiter rufiventris</i>		-	-				29	S	Simmons (1986)
<i>Diomedea immutabilis</i>	-	-	-				30	N	Rice & Kenyon (1962)
<i>Sula capensis</i>	+	-			0		32	S	Jarvis (1974)
<i>Sula capensis</i>	+	-					33	S	Navarro (1991)
<i>Falco tinnunculus</i>	+	0	0				34	S	this study
<i>Ficedula hypoleuca</i>	+	-	-		0	0	40	N	Sanz (1997)
<i>Passer domesticus</i>	+	-	0		0	0	40	N	Hegner & Wingfield (1987)
<i>Troglodytes aedon</i>	+	0	0		0	0	40	N	Finke, Milinkovich & Thompson (1987)
<i>Troglodytes aedon</i>	+	-				0	40	N	Robinson & Rotenberry (1991)
<i>Eudiptula minor</i>	+	-	0				40	S	Dann (1988)
<i>Puffinus tenuirostris</i>	0	-	-				41	S	Norman & Gottish (1969)
<i>Agelaius phoeniceus</i>	+	-	-				42	N	Cronmiller & Thompson (1980)
High latitudes (46° - 90° latitude)									
<i>Larus glaucescens</i>	+		0				50	N	Vermeer (1963)
<i>Fratercula arctica</i>	-		-				50	N	Nettleship (1972)
<i>Larus argentatus</i>	+	0	0				50	N	Haymes & Morris (1977)
<i>Falco sparverius</i>	+	-					50	N	Gard & Bird (1992)
<i>Ficedula hypoleuca</i>	+	-	0	0			51	N	Von Haartman (1954)
<i>Parus caeruleus</i>	+		0	0	-	0	51	N	Nur (1984a, 1984b, 1988b)
<i>Alca torda</i>	+	-	-				51	N	Lloyd (1977)
<i>Delichon urbica</i>	+	0	0				51	N	Bryant (1975)
<i>Fratercula arctica</i>	+		-				52	N	Corkhill (1973)
<i>Columba palumbus</i>	+	-	-	0			52	N	Murton, Westwood & Isaacson (1974)
<i>Passer domesticus</i>	+	-	-				52	N	Schifferli (1978)
<i>Apus apus</i>	-		-				52	N	Perrins (1964)
<i>Parus major</i>	+					0	52	N	Boyce & Perrins (1987); Pettifor, Perrins & McCleery (1988)
<i>Larus fuscus</i>	+	0	0				52	N	Harris & Plumb (1965)
<i>Branita canadensis</i>	0	0	0	0	-	-	53	N	Lessels (1986)
<i>Falco tinnunculus</i>	+	-	-	0	-	0	53	N	Dijkstra, <i>et al.</i> (1990)
<i>Ficedula hypoleuca</i>	0	-	-		-	-	55	N	Askenmo (1977, 1979)
<i>Parus major</i>	+	-	-	-		-	55	N	Smith, Kallander & Nilsson (1987, 1989)
<i>Corvus corone</i>	+	0	-				55	N	Loman (1980)
<i>Sula bassna</i>	+		-				56	N	Nelson (1964)
<i>Pica pica</i>	-	0	-				56	N	Hogstedt (1980)
<i>Ficedula hypoleuca</i>	+	-	-		-		56	N	Kallander & Smith (1990)
<i>Delichon urbica</i>	+	-	-				56	N	Bryant & Westertierp (1983)
<i>Cepphus grylle</i>	+	0	0				57	N	Asbirk (1979)
<i>Ficedula albicollis</i>	+			-		0	57	N	Gustafsson & Sutherland (1988)
<i>Stercorarius longicaudus</i>	+		0				60	N	Andersson (1976)
<i>Corvus frugilegus</i>	+					0	62	N	Roskaft (1985)
<i>Aegolius funereus</i>	+	0	0		0	0	63	N	Korpinaki (1988)
<i>Pica pica</i>		0	0	-			63	N	Husby (1986)
<i>Turdus pilaris</i>	+	0	0				63	N	Slagsvold (1982)

DISCUSSION

Among Common Kestrels studied by Dijkstra *et al.* (1990) in the Netherlands, a high latitude environment, nestlings in enlarged broods had slower growth rates and higher mortality rates than control broods. Nonetheless, parents were still able to fledge more young than determined by natural clutch size. As in this study, these birds were able to increase their provisioning rate by both parents allocating more time to hunting for the brood, resulting in enlarged broods receiving as much food per nestling as control broods. Unnaturally large broods did, however, have a negative impact on fledgling survival and reproductive success of the adults in the following year. Prey population dynamics are different at different latitudes (Hansson & Henttonen 1985) and it is possible that prey availability is lower at mid- or low latitudes (Beissinger 1990). This study showed, however, that kestrels are able to raise artificially increased broods, suggesting that clutch size is not limited by the ability of adults to provision offspring. However, this study could not determine whether such provisioning compromised future reproductive output of the adults.

Kestrels can increase the amount of food delivered to a nest by increasing their time spent hunting, increase the proportion of hover hunting to perch hunting, increasing their strike rate or by catching larger prey. Most hunting was away from the nest, so hunting duration was not recorded in this study and nor were strike rate and prey capture success. Parents of enlarged broods spent on average more time away from the nest than parents of control and reduced broods (Fig. 2). As there was a significant correlation between provisioning rate and time away from the nest, these results suggest that strike rate and prey capture success were similar between control and manipulated broods and that the differences in food deliveries were due to differences in the time spent hunting. A comparison of the number of prey items provisioned per day (Fig. 6a) and the number of grams provided to the brood per day (Fig. 6b) could be used to determine whether the increased time hunting was used only to increase the number of prey provisioned or if there was also an increase in the size of prey brought to the nest. The extent of increase in the number of prey items delivered per day and the number of grams of prey provisioned per day did not differ, indicating that parents increased the amount of food for the nestlings by increasing the hunting time and thus the number of prey items caught. There was no difference in the frequency of prey delivered for the various size categories (Table 2), nor for the proportions of vertebrate and invertebrate prey (Table 3) between the manipulations.

Parents of enlarged broods were able to provide as much food per nestling to their brood as control pairs (Fig. 6c). Evidence from this study suggests that kestrels at mid-latitudes are easily able to provision enough food to their chicks. If the females were under pressure to provision more food to enlarged broods, it would have been expected that they would have spent a proportion of their time hunting around the nest site while attending the brood. Females hunted more than males at the nest site but those tending enlarged broods did not make more strikes there than females with control and reduced broods.

When surplus food is available, kestrels cache food during the breeding season to spread the food delivery to the nest throughout the day and to exploit hunting opportunities during the best time of day (Village 1990). In this study, food was delivered regularly throughout the day by males in control and manipulated broods. This suggests that food was not cached because of food resources only being available during certain hours of the day. In situations where food was short, parent kestrels fed prey items directly to the brood rather than cache food. Although kestrels provisioning enlarged broods did cache some prey, most prey caching was recorded for the control and, especially, the reduced broods. This suggests that broods of six or seven are close to the maximum size that the kestrels were able to successfully raise. The advantages of food surpluses, as seen in reduced broods, may be reflected later by allowing the parents to be in better condition the following breeding season or to have a second brood in the same season (Van Heerden *et al.* 1994).

Dijkstra *et al.* (1990) showed that male kestrels tending reduced broods reduced their hunting time and females virtually stopped hunting. The response of parents to reduced broods in this study varied. Some pairs were no different to control birds in terms of nest attendance and provisioning

rates. Individual nestlings in reduced broods received on average more food than control and increased broods due to the fewer nestlings in the nest (Fig. 6c) although this was not reflected in chick growth or fledging success.

Clutch and brood sizes increase with latitude within and among several bird species (Payne 1976; Ricklefs 1980; Hessel 1985) and it has been suggested that food availability constrains clutch sizes at low latitudes (Simmons 1986; Beissinger 1990). The purpose of this study was to test whether birds at mid-latitudes are able to raise enlarged broods. Most brood manipulation studies have been conducted at high latitudes (Table 4) making latitudinal comparisons difficult. Results of the brood manipulations suggest that clutch sizes of birds at low and mid-latitudes are constrained, possibly by food supply, but also that parents fare better raising smaller broods. Other factors may also be involved. For instance, reduced offspring survival in enlarged broods of Barn Swallows *Hirundo rustica* has been attributed to a lowered immunocompetence (Saino *et al.* 1997).

This study does not support the hypothesis that brood size at mid-latitudes is regulated by food availability. However, there are several studies which do provide evidence in support of this hypothesis (Simmons 1986; 1989a; 1997). American Kestrels at a high latitude (50°N) were able to successfully raise enlarged broods during a year with high rodent numbers but not in a poor year (Gard & Bird 1992). However, Common Kestrels in Finland (63°N) were unable to successfully raise enlarged broods in both good and bad vole years (Korpimäki & Rita 1996). My own study on Common Kestrels was conducted during one season to minimize seasonal effects on the experimental manipulation and it is possible that it was conducted in a particularly "good" year, resulting in better success than normal. However, there are no data to support this and rodent counts conducted by Jarvis in the Cape Peninsula nature reserve were not unusually high during the year of this study (*pers. comm.*). Common Kestrels lay on average smaller clutches in South Africa than in Europe (Van Zyl 1994) but are able to raise larger broods (this study). The restraint to produce larger broods could possibly be due to having more than one brood per season as has been recorded in the study area (Van Heerden, *et al.* 1994) or because they live longer than their high latitude counterparts.

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