A brood-size manipulation experiment with Peregrine Falcons, *Falco peregrinus*, near Canberra

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Abstract.   Brood sizes of Peregrine Falcons in south-eastern Australia were manipulated to examine the effects on parental foraging effort and offspring growth rate. In broods enlarged by one, nestling growth rates were not affected but parents responded by bringing larger prey species and more biomass than did parents of control or reduced broods. Prey size and biomass decreased for the reduced brood. We conclude that parents appeared to increase hunting efforts to meet greater demands for food, and decrease hunting efforts for the reduced brood, but that direct observation of hunting behaviour by colour-marked and radio-tagged Peregrine Falcons with enlarged, reduced, and natural broods is necessary to determine how parents respond.

Introduction

Theories of the evolution of offspring size and number are dominated by two approaches, framed respectively as the Reproductive Effort Model and the Parent–Offspring Conflict Model. For the first approach, Lack (1947) suggested that altricial birds should lay the clutch that fledges the most offspring, and suggested brood manipulations as a direct experimental test of the hypothesis. Modern reviews of clutch size theory (Stearns 1992) assess deviations from the Lack theory as trade-offs that arise from brood parasitism, parent–offspring conflict (Trivers 1974), temporal variation in optimal clutch size and other forms of variance in parental or offspring life-history traits that translate to game theory (Mock *et al.* 1998).

Many support Lack's view that the most common clutch size is typically the most productive, and that deviations from this are explained by parent–offspring conflict. However, a more convincing argument by Hogstedt (1980) is for individual optimisation of brood size by parents, an approach amenable to experimentation. As experimental evidence is the most informative test of ecological theory (Rohner and Smith 1996), Lack's direct approach is well suited to fundamental questions on the determinants of reproductive investment with enlarged broods.

There are several implicit but frequently untested assumptions for the Reproductive Effort Model: (1) Do parents display a functional response to enlarged broods? If so, do they supply extra food to additional nestlings or partition the same amount of food among the brood? (2) What are the consequences for increased or reduced broods in terms of growth rates, survival, or recruitment to the breeding population? Reviews have framed these questions for birds in general (Lindén and Møller1989; Dijkstra *et al.* 1990), but

only recently have there been reviews of brood manipulations for diurnal raptors including kestrels, gyrfalcons, sparrowhawks, harriers, snail kites, savanna hawks, Wahlberg's eagles and ospreys (Simmons 2002). On brood enlargement, seven species increased their provisioning rate, one species decreased its provisioning rate, and five species showed no change. It is interesting that in breeding events said to be set by density dependence, with home-range and territory size set by food availability (Newton 1979, 1989), extra food is available to feed some artificially enlarged broods. However, Simmons pointed out that per-nestling biomass decreased in the increased broods. Although no formal meta-analysis was undertaken, clearly more studies are required for any definitive patterns to emerge. There are potentially confounding effects from predators, weather, or frequent manipulations and/or nestling measurements that could influence the behaviour of females especially, whether they hunt for extra nestlings or stay and protect them.

In the literature on brood manipulation there are no studies of raptors in Australia and, surprisingly, no studies of Peregrine Falcons, *Falco peregrinus*, though the species is an excellent model for testing such questions. Transferral of nestling Peregrine Falcons among broods is a common management technique (Cade *et al.* 1988), as Peregrine Falcons are long-lived species that readily accept extra young placed in their nests and feed them with their own.

The aim of the present study was to manipulate Peregrine Falcon broods to test the effects on offspring growth and parental foraging effort. We quantify differences in nestling growth and prey brought to nests of Australian Peregrine Falcons with artificially enlarged, reduced, and control broods. We examined whether quantity and size of prey items differed between (1) broods before, during, and after

they were manipulated, (2) manipulated and unmanipulated broods during the manipulation period, and (3) broods of different sizes during the manipulation period. The confirmatory hypotheses are that (i) parents of enlarged broods would respond, not by bringing more prey items of the same size but by bringing larger species of prey to the young, (ii) parents of the reduced brood would bring smaller prey, and (iii) growth rates of nestlings would be unaffected. The study contributes new information to the literature on the response of parents to altered brood sizes and provides data on a species that is otherwise very well known.

Methods

During the 1991 breeding season, five Peregrine Falcon nests were visited near Canberra at approximate 3-day intervals to measure young and collect prey remains. At the first visit to a brood, the nestlings' ages were determined at hatching or by wing length (Olsen and Olsen 1987). Nestlings were marked with a marking pen, and later a leg band, and weighed to the nearest gram with a spring balance. We measured the unflattened wing length to the nearest millimetre with a ruler. To minimise disturbance, we approached from the same direction and kept visits to <15 min; we did not stay to observe adult behaviour.

Brood size of Peregrine Falcons in Australia varies from 1 to 4, though broods of 4 are uncommon. Average brood size is 2.24 in Victoria and 2.14 in the Canberra area (Pruett-Jones *et al.* 1980; Olsen and Olsen 1989). Nests A, B and C started with 3 young each. At about Day 15, 2 females were transferred from Nest A, 1 each to Nests B and C. The manipulation left Nest A with 1 male, Nest B with 4 females, and Nest C with 3 females and 1 male (Table 1). At about Day 30, the 2 transferred females were returned to the original nest (Nest A) so that we could weigh all nestlings and collect prey remains after the manipulation period and all young would fledge from their original nests. Two other nests were unmanipulated controls for prey analysis and nestling growth rates: Nest D with 1 male and 2 females, and Nest E with 2 females (Table 1). No data were available on other Peregrine Falcon broods for the Canberra region in the same year, but comparative growth data were available for three wild broods measured in the same area in 1982 (1 male, 1 female), 1983 (3 females), and 1992 (2 females, 1 male), giving a total *n* for nestling growth of 22.

Diet

Prey remains and pellets were collected from nest ledges and cliff tops immediately above or within 5 m either side of the nest. Regurgitated pellets as well as bones and feathers were analysed to minimise any potential biases in estimates of overall diet (Simmons *et al.* 1991).

We separated and sorted feathers, castings and bones. Feathers were identified by microscopy, based on key features in Brom (1986) and Day (1966), and morphology/colour comparisons of frozen bird specimens. Bones were identified by morphological comparisons to museum specimens. Castings were soaked and separated by the foregoing methods to identify species. Counts of bones, feet, and primary and tail feathers, as in Olsen *et al.* (1993), allowed estimates of prey numbers. We did not assume that one casting represented one prey bird since nestlings share prey items and more than one species was often found in each casting.

Estimates of prey biomass were derived from the weights of specimens in the Australian National Wildlife Collection, live birds (A. Rowells, personal communication) and road kills. For the six commonest prey species, the following weights were used as representative: Rock Dove, *Columba livia* (all were banded racing pigeons), 465 g; Galah, *Cacatua roseicapilla*, 335 g; Silver Gull, *Larus novaehollandiae*, 321 g; Crimson Rosella, *Platycercus elegans*, 130 g; Eastern Rosella, *Platycercus eximius*, 105 g; and Common Starling, *Sturnus vulgaris*, 75 g.

Bird-catching falcons take prey averaging about 20% of the falcon's weight (Boyce 1985). To a 650-g male Peregrine Falcon in the Canberra region (Olsen, unpublished), this percentage would equate to prey mass of 130 g, and to a 950-g female about 190 g. Applying the 20% rule-of-thumb (Boyce 1985) to this estimated size, we classed prey species as small if <160 g and large if >160 g.

We collected the prey items brought to nests during the pre-manipulation, manipulation, and post-manipulation phases. Each visit corresponded to nestling age, not calendar date, as it was not feasible to visit all nests in a single day. At the first visit to the brood, the cliff above the nest and nest ledge were cleared of earlier remains. This first collection was not considered for analysis as the remains had accumulated over the preceding months. We collected prey remains during the pre-manipulation phase at about Day 10. Nestlings were transferred at about Day 15 and prey remains were collected during manipulation at about Days 18, 21, 24, 27, and 30. At about Day 30, nestlings were transferred back to original nests, and prey collected for the post-manipulation phase about 1 week after young fledged and again when fledglings were about 70 days old.

Before, during and after the manipulation period, we compared (1) prey size categories, (2) number of prey items, and (3) biomass, as determined by numbers of prey multiplied by a characteristic weight for each species. Within the manipulation period, we compared (4) the number and type of prey species for broods of different sizes.

Nestling growth

To assess the effects of brood enlargement on nestling growth, we compared wing length and weight of controls, including the single male in the reduced brood, and enlarged broods. Mean growth rate per day was calculated as the gain in wing length or mass divided by the elapsed time in days. Because of sexual dimorphism, we compared growth rates of control and enlarged broods by paired *t*-tests separately for males and females.

Results

The diet consisted almost entirely of birds, ranging in size from approximately 23 g to 465 g. Six prey species (Common Starlings, Silver Gulls, Rock Doves, Galahs, Crimson and Eastern Rosellas) constituted 90.4% of the diet by number and 93.5% of the total prey biomass (Table 2). A minute proportion of the diet consisted of insects. It was possible that insect remains came from the stomachs of insectivorous birds, but insect remains were sometimes found when no insectivorous birds occurred in the diet.

Peregrine Falcons tend to bring more large prey to young in the second half of the nestling phase (equivalent to the

Table 1.   Brood size of Peregrine Falcon young at the five nests used for prey analysis during each treatment phase of the experiment

Nest	Pre-treatment Days 1–15	Treatment Days 16–30	Post-treatment Days 31+
A	3	1	3
B	3	4	3
C	3	4	3
D	3	3	3
E	2	2	2

Table 2.   Bird species found as prey remains at five nests of Peregrine Falcons near Canberra in 1991

Species	*n*	% of prey by number	% of prey by biomass
Silver Gull, *Larus novaehollandiae*	31	15.5	27.6
Rock Dove, *Columba livia*	7	3.2	9.6
Galah, *Cacatua roseicapilla*	27	13.4	26.5
Crimson Rosella, *Platycercus elegans*	20	10.7	7.9
Eastern Rosella, *Platycercus eximius*	25	13.4	7.8
Common Starling, *Sturnus vulgaris*	64	34.2	14.1
% sub-total		90.4	93.5
Stubble Quail, *Coturnix pectoralis*	2	1.1	0.6
Masked Lapwing, *Vanellus miles*	1	0.53	1.1
Nankeen Kestrel, *Falco cenchroides*	1	0.53	0.5
Common Bronzewing, *Phaps chalcoptera*	1	0.53	0.9
Red-rumped Parrot, *Psephotus haematonotus*	3	1.6	0.5
Grey Shrike-thrush, *Colluricincla harmonica*	2	1.1	0.4
Magpie-lark, *Grallina cyanoleuca*	2	1.1	0.5
Richards Pipit, *Anthus novaeseelandiae*	2	1.1	0.1
Pied Currawong, *Strepera graculina*	1	0.53	0.8
Unidentified passerines	2	1.1	0.3
European Rabbit, *Oryctolagus cuniculus*	1	0.53	0.9
% sub-total		9.6	6.6
	Total items = 187		Total biomass = 34098 g

manipulation and post-manipulation phases in this study), often because females begin to hunt (Olsen and Stephenson 1996). This is reflected in Table 3. However, during the manipulation phase, we recorded no large prey brought to the reduced brood, and slightly more large prey brought to increased broods than to control broods. Across the pre-manipulation, manipulation and post-manipulation phases, we collected more prey items from enlarged broods than from control broods or from the single reduced brood (90, 73 and 27 prey items respectively) (Table 3).

Fig. 1 shows that parents of larger broods increased their capture of larger birds such as Silver Gulls, Rock Doves and Galahs. During the manipulation phase there was less mean biomass found in nests with reduced and control broods than in nests of enlarged broods, and fewer species in the nests with the reduced brood (only Common Starlings, Crimson Rosellas, and Eastern Rosellas, no Galahs, Rock Doves, or Silver Gulls even though the reduced brood was close to a lake where Silver Gulls and Galahs were common). After the

manipulation phase, as expected for Peregrine Falcons in the late nestling stage (Olsen and Stephenson 1996), we found an increase in the percentage of large prey brought to all nests (Table 3). The number of prey species and mean biomass collected at nests with more nestlings was higher (Fig. 1). The reduced brood (1 nestling) received less biomass during the manipulation period than did the two control broods (2 and 3 nestlings), or the two increased broods (4 and 4 nestlings), and slightly more biomass per nestling for reduced broods than for control and increased broods (Table 4).

Growth of nestlings in controls (natural broods and the single male in the reduced brood) and in enlarged broods was similar (Fig. 2). There were no significant differences for growth rates between control and enlarged broods for weight (for males, paired $t = 1.28$, d.f. $= 4$, $P = 0.27$; for females, $t = 0.10$, d.f. $= 11$; $P = 0.91$) or wing length (males, $t = 0.48$, d.f. $= 4$, $P = 0.65$; females, $t = 0.60$, d.f. $= 11$, $P = 0.56$).

Table 3.   Summary of prey type data taken by Peregrine Falcons, comparing manipulation phase (pre-manipulation, manipulation, post-manipulation), brood manipulation (reduced, control, or enlarged brood), and prey size (small, large)
Numbers in parentheses are the percentages of small or large prey for the manipulation phase and brood type

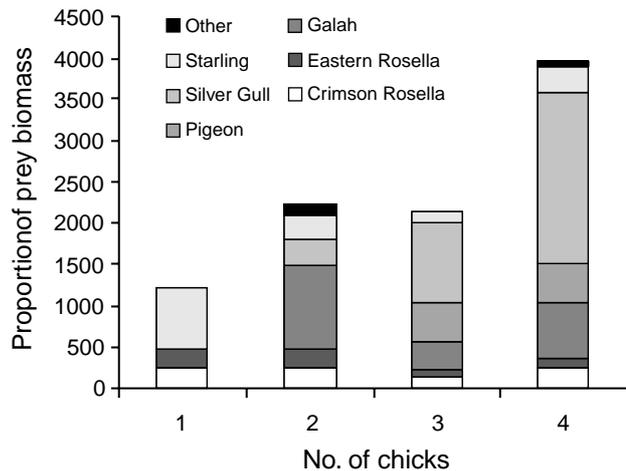| Brood manipulation	Pre-manipulation phase		Manipulation phase		Post-manipulation phase	
	Small	Large	Small	Large	Small	Large
Reduced	6 (86%)	1 (14%)	14 (100%)	0 (0%)	4 (67%)	2 (33%)
Control	14 (82%)	3 (18%)	14 (61%)	9 (39%)	19 (58%)	14 (42%)
Enlarged	21 (75%)	7 (25%)	18 (50%)	18 (50%)	11 (42%)	15 (58%)
Totals	41 (79%)	11 (21%)	46 (63%)	27 (37%)	34 (62%)	31 (38%)

Fig. 1. Biomass of different prey species in reduced, control and enlarged broods. Blocks on the histogram represent the proportional contribution of each species to the total biomass for each brood size. Data come from the manipulation period (21–35 days of age).

Discussion

While there was clear evidence of a parental response in provisioning effort, the sparse sample sizes do not allow for generalisation beyond the scope of this study. However, equivalent results have been confirmed in other falcons (e.g. Poole 1988; Masman *et al.* 1988; Korpimäki 1988; Dijkstra *et al.* 1990; Gard and Bird 1990, 1992). On brood enlargement, many raptor species increased their provisioning rate (Simmons 2002). Extra food was available to feed artificially enlarged broods even in breeding events said to be set by density dependence, with home range and territory size set by food availability (Newton 1979, 1989). A possible explanation is that dimorphic raptors have a buffer against temporal food shortage in the form of a prey refuge. Larger prey is left in the territory during the first half of the nestling phase when the male hunts for the female and brood but females do not hunt, then later is caught by females or males in the second half of the nestling phase (Olsen 1992).

Table 4. Biomass (a) per brood size for broods of different sizes, and (b) per nestling in the reduced, control and increased broods
Data are from the manipulation period (21–35 days of age)

	Biomass (g)
(a) Brood size	
1 nestling	545
2 nestling	2220
3 nestling	2148
4 nestling	3957
(b) Brood manipulation	
Reduced brood (1 nestling)	1220
Control brood (5 nestlings)	873.6
Increased brood (8 nestlings)	989.35

In this study, fewer species and numbers of prey were brought to the reduced brood, suggesting that the male continued to bring small prey but the female ceased hunting, as reported for Eurasian kestrels with reduced broods (Dijkstra *et al.* 1990). During the manipulation phase, parents of larger broods enlarged their capture of large prey (Silver Gulls, Rock Doves and Galahs) compared with the pre-manipulation phase or controls (Table 3, Fig. 1). While our study is the first to note that larger prey were brought to artificially enlarged broods, many other studies have involved raptors (e.g. kestrels) that targeted rodents, and kestrels are less dimorphic than Peregrine Falcons. There is evidence that successfully breeding pairs of some raptors capture larger prey during the breeding season than do non-breeding pairs, for example, Spotted Owls, *Strix occidentalis* (Barrows 1987; Thrailkill and Bias 1989).

Earlier studies have shown that females can take larger prey than males (Newton 1986; Poole and Boag 1988; Andersson and Norberg 1989; Ratcliffe 1993) and that females adjust their provisioning effort to the foraging ability of their mates (Newton 1979; Tolonen and Korpimäki 1994; Rohner and Smith 1996). In this study, the provisioning burdens of the parents were increased by artificially enlarging the broods. However, the alternative explanation, that larger prey items are provisioned by males, is not precluded by the dive-bombing hunting tactics of Peregrine Falcons (Debus 1998). Galahs are 50% of the weight of the average male, far above the average 20% suggested by Boyce (1985), and are potentially dangerous quarry because of the Galah's agility and powerful beak (Olsen 1974), and are more difficult to carry to the nest.
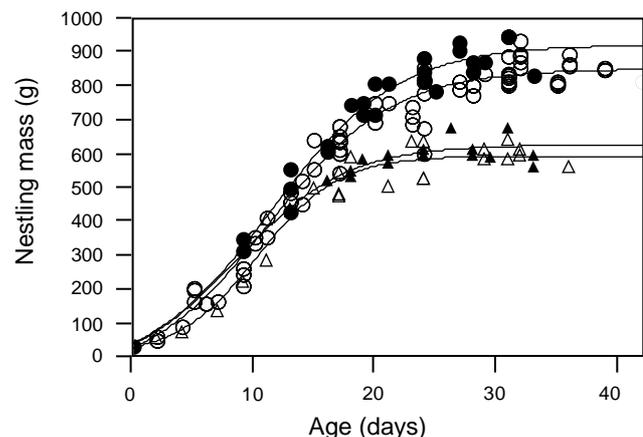

Fig. 2. Weights of 22 nestling Peregrine Falcons plotted against age. Curves were fit by iteratively weighted least-squares regression to a sigmoid function: all curves had $r^2 > 0.96$. From top to bottom, the black circle and upper curve depict females in enlarged broods, white circles and second curve depict females in control broods, black triangles and third curve depict males in enlarged broods, and the white triangles and bottom curve depict males in control broods. Overlapping standard errors for the mean growth coefficient indicated no significant differences by sex or by treatment for the growth parameters.

Female Ospreys with artificially increased broods stayed with nestlings because of risks of predation, ate less, and gave the remaining portion to the brood (Poole 1989). Both parents lost weight tending larger broods, but females lost about three times as much as males, a potentially drastic 40% if the rate of loss had continued for 30 days. In circumstances of perceived danger from predators, females were reluctant to leave young in the nest unguarded. Thus, females with artificially enlarged broods may have different ways of buffering against food shortage.

Lifetime reproductive output in raptors depends greatly on how long the raptor lives (Newton 1989): the longer they live, the more young they are likely to fledge. Bird-catching raptors may die from collisions and other accidents while hunting (Olsen 1989), hence males and females reduce their energetic outputs and mortality risks by hunting as little as possible. These factors form conflicting interests in the allocation of parental effort between sexes as well as between offspring and parent. Male Eurasian Kestrels reached maximum daily energy expenditures and suffered greater mortality when broods were enlarged, although the mechanisms for this trade-off are unknown (Masman *et al.* 1989; Dijkstra *et al.* 1990). However, Korpimäki and Rita (1996) found that weights of parent Eurasian Kestrels with enlarged broods were not affected, but the future survival of females declined, while the future survival of females with reduced broods increased. This was not the case for males.

As when Rohner and Smith (1996) enlarged broods of Great-horned Owls by 50% to three, our study observed no effects on nestling growth when a single young was added, enlarging broods of Peregrine Falcons by 33% to four. When they doubled the brood size to four, Rohner and Smith (1996) reported that growth rates of owl nestlings fell below normal. Had we doubled the brood sizes of Peregrine Falcons in this study to six, it is likely that growth would have been lower than normal. Growth rates of nestlings were not affected by enlarging broods of American Kestrels (Gard and Bird 1990) or Gyrfalcons (Poole 1988). This contrasts with the reduced growth rates of nestlings in enlarged broods of European Kestrels (Dijkstra *et al.*1990; Korpimäki and Rita 1996) and African Red-breasted Sparrowhawks (Simmons 1986). Such differences may relate to the risk of predation, level of interference from researchers, the percentage that broods were enlarged, and the geographic region where the experiment was conducted. Though Simmons (2002) argued that per-nestling biomass is the critical measure in these manipulation studies, we would argue that nestling growth is a more reliable and critical measure.

Conclusions

Peregrine Falcons in this study appeared to respond to artificially enlarged broods by bringing in larger prey. Direct observation of hunting behaviour by colour-marked and radio-tagged Peregrine Falcons with enlarged, reduced, and natural broods is necessary to determine if and how one or both parents respond. Further investigation will help determine whether larger prey is more available than smaller prey, or more energetically efficient, though more dangerous, for adults to capture. How females respond to artificially enlarged broods may depend on the female's assessment of risk to her nestlings from predators, including humans, and inclement weather.

References

Andersson, M., and Norberg, R. A. (1981). Evolution of reversed sexual size dimorphism and role partitioning among predatory birds, with a size scaling of flight performance. *Biological Journal of the Linnean Society* **15**, 105–130.

Barrows, C. W. (1987). Diet shifts in breeding and non-breeding Spotted Owls. *Journal of Raptor Research* **21**, 95–97.

Boyce, D. A. (1985). Prairie Falcon prey in the Mojave Desert, California. *Journal of Raptor Research* **19**, 129–134.

Brom, T. G. (1986). Microscopic identification of feathers and feather fragments of Palaearctic birds. *Bijdragon tot de Dierkunde* **56**, 181–204.

Cade, T. J., Enderson, J. H., Thelander, C. G., and White, C. M. (Eds) (1988). 'Peregrine Falcon Populations: Their Management and Recovery.' (The Peregrine Fund Inc.: Boise, ID.)

Day, M. B. (1966). Identification of hair and feather remains in the gut and faeces of stoats and weasels. *Canadian Journal of Zoology* **148**, 201–217.

Debus, S. (1998). 'The Birds of Prey of Australia – A Field Guide.' (Oxford University Press: Melbourne.)

Dijkstra, C., Bult, A., Bijlsma, S., Dann, S., Meijer, T., and Zilstra, M. (1990). Brood size manipulations in the Kestrel *Falco tinnunculus*: effects on offspring and parent survival. *Journal of Animal Ecology* **59**, 269–286.

Gard, N. W., and Bird, D. M. (1990). Breeding behaviour of American Kestrels raising manipulated broods in years of varying prey abundance. *Wilson Bulletin* **102**, 605–614.

Gard, N. W., and Bird, D. M. (1992). Nestling growth and fledging success in manipulated American Kestrel broods. *Canadian Journal of Zoology* **70**, 2421–2425.

Green, D. J., and Ydenberg, R. C. (1994). Energetics of male Ospreys provisioning natural and manipulated broods. *Ardea* **82**, 249–262.

Hogstedt, G. (1980). Evolution of clutch size in birds: adaptive variation in relation to territory size. *Science* **210**, 1148–1150.

Korpimäki, E. (1988). Clutch size, breeding success and brood size experiments in Tengmalm's Owl *Aegolius funereus*: a test of an hypothesis. *Ornis Scandinavica* **18**, 277–284.

Korpimäki, E., and Rita, H. (1996). Effects of brood size manipulations on the offspring and parental survival in the European Kestrel under fluctuating food conditions. *Ecoscience* **3**, 264–273.

Lack, D. (1947). The significance of clutch size. *Ibis* **89**, 302–352.

Lindén, M., and Møller, A. P. (1989). Cost of reproduction and covariation of life history traits in birds. *Trends in Ecology and Evolution* **4**, 367–371.

Masman, D., Daan, S., and Dijkstra, C. (1988). Time allocation in the Kestrel *Falco tinnunculus*, and the principle of energy minimization. *Journal of Animal Ecology* **57**, 411–432.

Mock, D. W., Parker, G. A., and Schwagmeyer, P. L. (1998). Game theory, sibling rivalry, and parent–offspring conflict. In 'Game Theory and Animal Behavior'. (Eds L. A. Dugatkin and H. R. Reeve.) pp. 146–167. (Oxford University Press: Oxford.)

Newton, I. (1979). 'Population Ecology of Raptors.' (Poyser: Berkhamsted, UK.)

Newton, I. (1986). 'The Sparrowhawk.' (Poyser: Calton, UK.)

Newton, I. (1989). 'Lifetime Reproduction in Birds.' (Academic Press: London.)

Olsen, J. (1974). Investigation into the biology of the Peregrine Falcon and Black Falcon in the Port Augusta–Wilmington area, South Australia. Report, South Australian Nationall Parks and Wildlife Service.

Olsen, J. (1989). Some thoughts on risk of accidents in raptors. *Australian Raptor Association News* **10**, 69–72.

Olsen, J. (1992). Does the breeding system of some raptors help to maintain a buffer against food shortage? *Australian Raptor Association News* **13**, 66–67.

Olsen, J., and Stevenson, E. (1996). Female Peregrine Falcon replaces an incubating female and raises her young. *Australian Bird Watcher* **16**, 205–210

Olsen, P. D., and Olsen, J. (1987). Estimating the age of nestling raptors. *Australian Bird Watcher* **12**, 130–131.

Olsen, P., and Olsen, J. (1989). Breeding of the Peregrine Falcon: II. Weather, nest quality and breeding success. *Emu* **89**, 6–14.

Olsen, P., Olsen, J., and Mason, I. (1993). Breeding and non-breeding diet of the Peregrine Falcon near Canberra, prey selection, and the relationship between diet and reproductive success. In 'Australian Raptor Studies'. (Ed: P. D. Olsen). pp. 55–77. (Australian Raptor Association & Royal Australasian Ornithologists Union: Melbourne.)

Poole, A. F. (1989). 'Ospreys: A Natural and Unnatural History.' (Cambridge: New York.)

Poole, K. G. (1988). Feeding response by Gyrfalcons to brood size manipulations. *Journal of Raptor Research* **22**, 67–70.

Poole, K. G., and Boag, D. M. (1988). Ecology of Gyrfalcons, *Falco rusticolus*, in the central Canadian Arctic: diet and feeding behaviour. *Canadian Journal of Zoology* **66**, 334–344.

Pruett-Jones, S. G., White, C. M., and Devine, W. R. (1980). Breeding of the Peregrine Falcon in Victoria, Australia. *Emu* **80**, 253–267.

Ratcliffe, D. (1993). 'The Peregrine Falcon.' 2nd Edn. (Poyser: Calton, UK.)

Rohner, C., and Smith, J. N. (1996). Brood size manipulations in Great-Horned Owls *Bubo virginianus*: are predators food limited at the peak of prey cycles? *Ibis* **138**, 236–242.

Simmons, R. (1986). Food provisioning, nestling growth and experimental manipulation of brood size in the African Red-breasted Sparrowhawk *Accipiter rufiventris*. *Ornis Scandinavica* **17**, 31–40.

Simmons, R. E. (2002). Siblicide provides food benefits for raptor chicks: re-evaluating brood manipulation studies. *Animal Behaviour* **64**, 19–24.

Simmons, R. E., Avery, D. M., and Avery, G. (1991). Biases in diets determined from pellets and remains: correction factor for a mammal and bird eating raptor. *Journal of Raptor Research* **25**, 63–67.

Snyder, N. R. F., and Snyder, H. A. (1973). Experimental study of feeding rates of nestling Cooper's Hawks. *Condor* **75**, 461–463.

Stearns, S. C. (1992). 'The Evolution of Life Histories.' (Oxford University Press: Oxford.)

Thrailkill, J., and Bias, M. A. (1989). Diet of breeding and non-breeding California Spotted Owls. *Journal of Raptor Research* **23**, 39–41.

Tolonen, P., and Korpimäki, E. (1994). Determinates of parental effort: a behavioural study in the Eurasian Kestrel *Falco tinnunculus*. *Behavioural Ecology and Sociobiology* **35**, 355–362.

Trivers, R. L. (1974). Parent–offspring conflict. *American Zoologist* **14**, 249–264.

Zar, J. H. (1984). 'Biostatistical Analysis.' 2nd Edn. (Prentice-Hall: Englewood Cliffs, NJ.)