

Growth and survival of nestlings in a population of red-crowned parakeets (*Cyanoramphus novaehollandiae*) free of introduced mammalian nest predators on Tiritiri Matangi Island, New Zealand

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Abstract: The negative effects of introduced nest predators on the breeding success of endemic New Zealand parrots are well documented, as is their role in the general decline of these species. In contrast, little is known about the intrinsic intra-brood dynamics responsible for modulating fledging success in parrots breeding at sites free of introduced nest predators. We studied red-crowned parakeets over two breeding seasons on Tiritiri Matangi, an offshore island free of introduced mammalian predators. We analysed the patterns of hatching and survival, and sex-specific growth of nestlings in relation to clutch initiation date and natural levels of hatching asynchrony. We also explored the relationships of nestling sex and hatching rank on survival. Earlier laid clutches resulted in larger broods which in turn produced more nestlings in better body condition, independent of the sex of the nestlings. Similar to many other bird species with extensive hatching asynchrony, last hatched red-crowned parakeets suffered higher mortality than other hatch ranks. Primary sex ratios and sex ratios at hatching and fledging did not deviate significantly from parity. Our results indicate that in the absence of nest predation by exotic predators, the timing of clutch initiation and brood reduction due to starvation of last hatched nestlings are the most important determinants of nestling survival and growth in red-crowned parakeets. Consequently, from a conservation management perspective, close monitoring of target populations during the breeding season is recommended to estimate nestling survival and nest productivity when planning the timing of capture of wild birds for translocations or harvesting potential breeding stock for captive breeding programmes.

Keywords: conservation; hatching asynchrony; threatened species; mortality, parrot

Introduction

Parrots and cockatoos (Psittaciformes) represent one of the most endangered lineages of birds (Collar & Juniper 1991; Beissinger & Snyder 1992; Bennett & Owens 1997), with about 30% of all known species under various categories of conservation threat (Collar et al. 1994). Understanding psittacine reproductive biology is essential to identify and implement management strategies aimed at improving the breeding performance of individuals in remaining populations (White & Vilella 2004), increasing surviving population sizes (Clout et al. 2002; Vaugahn et al. 2005), and expanding the number of individuals and populations via translocations (Snyder et al. 1994). In recent years, there has been a vast increase in the number of studies with conservation relevance that document various aspects of the reproductive ecology of psittacines, including nesting requirements (Heinsohn et al. 2003; Murphy & Legge 2007) and mating systems (Erkstrom et al. 2007; Heinsohn et al. 2007). However, the ecological and anthropogenic factors limiting productivity of natural and managed populations of parrots are far from being understood.

Predation at the nest is the most critical limiting factor to fledging success in birds in general, and is commonly reported for parrots worldwide (González 2003; Murphy et al. 2003). Nest predators that affect breeding productivity of parrots include reptiles (Koenig 2001), birds (Pizo et al. 2008), and mammals (Renton & Salinas-Melgoza 2004), including humans

(González 2003). In addition to native nest predators, several parrots have suffered from additional pressure of exotic nest predators, such as rats (*Rattus spp.*), introduced by humans. Introduced predators have devastated many island ecosystems. They have reduced population sizes or caused the extinction of native psittacines on many insular sites, including Norfolk Island (Hill 2002), Macquarie Island (Taylor 1979), as well as on mainland and offshore New Zealand islands (Higgins 1999) in the southwestern Pacific, in Puerto Rico in the Caribbean, and elsewhere (Snyder et al. 1987).

The detrimental role of introduced nest predators on the productivity of New Zealand forest-dwelling parrots and other birds has been widely documented (Beggs & Wilson 1991; Lloyd & Powlesland 1994; O'Donnell 1996; Wilson et al. 1998). Currently, intensive management to control or eliminate introduced predators through trapping, poisoning, and shooting is at the centre of New Zealand conservation efforts (Towns & Broome 2003; Russell & Clout 2006). While positive effects of predator control on the expansion of parrot populations have been reported (Moorhouse et al. 2003; Ortiz-Catedral et al. 2009a), little is known about the role of intrinsic life-history factors such as timing of breeding, hatching asynchrony, and brood reduction, in regulating the reproductive output of parrots in areas free of introduced predators.

The red-crowned parakeet (*Cyanoramphus novaehollandiae*) is a vulnerable species endemic to New Zealand (Higgins 1999). Currently, the species mainly

inhabits offshore islands free of introduced mammalian predators (Higgins 1999). In addition to remaining natural and translocated wild populations, it is also bred in captivity by individuals and zoos under specific permits issued by the New Zealand Department of Conservation. Since the 1970s, there has been a growing interest in the potential for extensive captive propagation of red-crowned parakeets and their subsequent release into the wild, with a few failed attempts at establishing populations on mainland New Zealand (Dawe 1979; MacMillan 1990).

Red-crowned parakeets lay large clutches which hatch with variable degrees of asynchrony (Ortiz-Catedral 2006). These attributes make this species a good model to study the patterns and dynamics of nestling growth and survival in the absence of exotic nest predators. Information about the dynamics of breeding success, intra-clutch competition, and nest productivity is also valuable for a thorough assessment of captive breeding and timing of capture for translocation as conservation alternatives for red-crowned parakeets.

Other *Cyanoramphus* parakeets in New Zealand are threatened and difficult to study in the field due to their rarity, e.g. Malherbe's parakeet (*C. malherbi*) (Grant & Kearvell 2001; Ortiz-Catedral et al. 2009b), or remoteness of their populations, as in the case of the Antipodes Islands parakeet (*C. unicolor*) (West et al. 1995). Thus, having detailed information from a more common, closely related, and more accessible species can also assist those formulating conservation plans for other endangered taxa. Such an approach has been successful for another endangered New Zealand bird, the black robin (*Petroica traversi*) through study of the South Island robin (*P. australis australis*) (Butler & Merton 1992).

The aim of our study was to describe the pattern of growth and survival of red-crowned parakeet nestlings in relation to natural levels of hatching asynchrony on Tiritiri Matangi Island, where no introduced mammalian nest predators persist.

Methods

We conducted our study on Tiritiri Matangi Island, Hauraki Gulf, New Zealand (36° 36' S, 174° 53' E) over two breeding seasons: October 2004 to March 2005, and October 2005 to February 2006. Tiritiri Matangi is a 220 ha island covered with a mix of remnant coastal forest, replanted native vegetation patches, and grassland (Baber & Craig 2003). The island has been the focus of intense conservation-driven management including revegetation using native plant species and seed banks, the eradication of alien predators (Pacific rat or kiore, *Rattus exulans*) and the translocation of several endangered bird species (Rimmer 2004).

The red-crowned parakeet is a member of the subfamily Platycercinae (Boon et al. 2008) and it is the second largest *Cyanoramphus* species in New Zealand, measuring 23–28 cm in length and weighing 70–100 g. Males are larger than females, and beak measurements and morphology are routinely used to assign sex in the field (Sagar 1988). The species was reintroduced to Tiritiri Matangi in the 1970s (Dawe 1979) and is now common throughout the island. No instances of nest predation have been recorded since 2004, the beginning of our ongoing research on red-crowned parakeets on Tiritiri Matangi.

At the beginning of each breeding season, we searched for easily observed active nests in nesting boxes provided on the island and also in natural cavities (see Ortiz-Catedral & Brunton (2009a) for details on methodology). During the first

breeding season, study nests were visited every second day in order to detect clutch initiation date. After the hatching of the first egg, nests were visited daily until hatching of the last nestling. During the second breeding season, clutch initiation date was determined by backdating from the date of hatching of the first nestling, assuming an incubation period of 21 days and a 2-day interval between eggs (Ortiz-Catedral 2006). Hatching order was determined by opportunistic direct observation of hatching sequence or, if several nestlings had already hatched in a brood, hatching order was assigned retrospectively by looking at weight, dryness of feather down, feather development, and wing length. Wing length has been shown to be a good predictor of nestling age in a variety of psittacine species (Saunders 1986; Krebs 1999) and cross-checks were made with nestlings of known age to validate this approach (Ortiz-Catedral 2006). Total hatching asynchrony (i.e. time elapsed between hatching of first and last nestling in a brood, measured in days) was determined by recording the exact hatch sequence, or estimated by comparing ages of first vs. last hatched nestlings in broods where at least two eggs hatched ($n = 25$ broods).

Nestlings were classified as first, middle or last hatched retrospectively by considering brood size and degree of hatching asynchrony. For broods of four or more nestlings, more than one nestling was assigned to the same hatching rank: for example, a brood of six would consist of two first, two middle and two last hatched nestlings. For broods with an odd number of nestlings (i.e. 5 or 7 nestlings), hatching ranks were assigned considering hatching gap (in days) from the nearest nest mate (Krebs 1999). Nestlings were individually marked on the head with non-toxic colour markers to enable identification during nest checks. During every nest check nestlings were weighed to the nearest 0.01 g using a portable scale. We also measured wing length (from the base of right humerus to tip of largest primary feather). From ages 1–25 days, wings were measured to the nearest 0.1 mm with a dial calliper; subsequently, wings were measured with a plastic ruler to the nearest 1 mm. Finally, culmen length (from base of cere to tip of upper mandible) and tarsus length (right tarsus; outer joints) were measured with a dial calliper to the nearest 0.1 mm. Measurements were taken every two to three days during the first breeding season and once a week or once every two weeks during the second breeding season. Handling and measurements ceased when nestlings perched close to the entrance of the nest (34–39 days of age). This was to minimise premature fledging. After fledging, mass recession (i.e. proportion of weight loss from asymptotic mass to mass at the time of last weighing before fledging) could be calculated. Parameters among nestlings of different hatch ranks were used for descriptive purposes of the growth pattern of red-crowned parakeets, but were not compared statistically. This was due to the limited number of broods with at least three fledglings that were measured frequently enough to obtain estimates of growth rate, and due to the high level of clutch failure observed during the first breeding season (Ortiz-Catedral & Brunton 2008).

To describe the pattern of nestling growth of red-crowned parakeets we calculated growth curves for mass and wing for 13 nestlings (seven females and six males) from four broods found during the first breeding season. We used the logistic growth model (Ricklefs 1967). Curves were calculated separately for female and male chicks. For these nestlings, we collected enough measurements (10–15) before they fledged to fit growth curves. We used CurveExpert 1.3[®] to determine

the regression model that best fit our data.

For both seasons we also calculated a brood body-condition index based on the metric reported by Erksstrom et al. (2007). This index is defined by $\sqrt[3]{mf/t}$, where mf is the average pre fledging mass (g) of the brood and t is the average pre fledging tarsus length (mm) in the brood. We used this index for statistical comparisons between broods with different brood size, degree of hatching asynchrony, and clutch initiation date. Individual fledging age was assumed to occur halfway between the last nest check when a nestling was recorded in the nest and the following nest check. We only included 14 broods from both breeding seasons where at least three nestlings survived to fledging (to ensure there was at least one fledgling per hatch rank). These broods represented a total of 55 nestlings. For these same broods we recorded the number of dead nestlings during every nest visit to analyse the relationship between degree of hatching asynchrony and mortality. We also analysed the relationship between clutch initiation date, number of fledglings produced, and number of dead nestlings found in 47 broods during our two year study. Two nests which failed due to heavy rainfall were excluded (Ortiz-Catedral & Brunton 2008).

We analysed primary sex ratio, sex ratio at hatching, and sex ratio at fledging. The analysis of primary sex ratios was limited to nests with no more than one un-sexed embryo or nestling. For sex ratio at hatching and sex ratio at fledging we included all broods that fledged at least one chick. For primary sex ratio we collected a total of 103 samples for molecular determination of sex, including unhatched eggs ($n = 20$), tissue samples from dead nestlings ($n = 38$), and feathers from live chicks ($n = 45$). All samples were stored at -20°C . Molecular sexing of samples was completed at the Allan Wilson Centre for Molecular Ecology and Evolution (Massey University, Palmerston North, New Zealand) or by DNA Solutions (Wantirna, Victoria, Australia), following the methods of Griffiths et al. (1998).

During our study, samples from 15 nestlings could not be sexed using molecular methods and the chicks fledged before additional feathers for re-testing could be sampled. For these individuals, we assigned sex on the basis of culmen dimensions. The culmen length of DNA-sexed fledglings showed no overlap between males and females from 25 days of age (mean culmen length males = 14.83 ± 0.91 SD, $n = 11$; mean culmen length females = 12.09 ± 0.71 SD, $n = 13$; $t = -3.08$, $P = 0.002$) and, thus, was considered a reliable feature to determine sex. In total, we included 16 completely sexed broods for analysis of primary sex ratios. For sex ratio at hatching ($n = 18$), we excluded broods where more than one hatchling could not be sexed following Krebs (1999). For sex ratio at fledging, we included a further six broods sampled for molecular sexing (feathers only). From these samples, DNA could not be extracted from two individuals. Thus, we assigned sex using culmen size as above. Our analysis of sex ratio and sex-specific growth until fledging included 22 broods in total.

Normality of data sets was tested with Shapiro-Wilks test in SAS PROC UNIVARIATE Version 8[®]. When the data did not fulfil assumptions of parametric tests, alternative non-parametric tests were applied. We used StatView Version 5.0.1[®] for linear regression analysis of clutch size and total hatching asynchrony. To analyse the relationship between brood size, brood body-condition index, productivity, and mortality of broods in relation to clutch initiation date and degree of hatching asynchrony, we used nonlinear regression models in StatView Version 5.0.1[®]. Primary sex ratios, sex ratio at hatching and sex ratio at fledging (proportion of males

in all cases) were analysed by the binomial test (Wilson & Hardy 2002) using SAS PROC FREQ in SAS Version 8[®]. Mortality between nestlings of different hatching rank and sex was analysed using a Chi-square test in SAS PROC FREQ. Data presented are means \pm SD. We set $\alpha = 0.05$.

Results

Red-crowned parakeet clutches hatched over periods of 1 to 13 days. The degree of total hatching asynchrony was not consistent among clutches, with clutches of the same size hatching over different periods (Fig. 1). We detected a significant pattern of large clutches hatching over a longer period of time, i.e. they exhibited higher hatching asynchrony (linear regression $r^2 = 0.37$, $P < 0.01$, $n = 25$ clutches) (Fig. 1). We did not detect an effect of total hatching asynchrony on the mean body condition index of broods (body condition index $r^2 = 0.032$, $P = 0.52$, $n = 15$) (Fig. 2a) or on the mean time nestlings needed to attain asymptotic mass (age to reach asymptotic mass $r^2 = 0.004$, $P = 0.84$, $n = 14$) (Fig 2b). Total hatching asynchrony was not related to the number of fledglings produced per brood (polynomial regression $r^2 = 0.003$, $P = 0.85$, $n = 14$) (Fig. 2c) or the number of dead nestlings within a brood (polynomial regression $r^2 = 0.044$, $P = 0.47$, $n = 14$) (Fig. 2d).

Within broods we detected consistent sex differences, with males reaching higher values of asymptotic mass (Mann-Whitney (MW) $Z = 2.75$, $P < 0.01$, $n = 66$), age to reach asymptotic mass (MW $Z = 2.65$, $P < 0.01$, $n = 66$), pre fledging mass (MW $Z = 3.10$, $P < 0.01$, $n = 66$) and pre fledging wing length (MW $Z = 2.83$, $P = 0.05$, $n = 66$) (Table 1). In contrast, no significant differences were found for mass recession (g) (MW $Z = 0.48$, $P = 0.63$, $n = 66$), percentage of mass recession (MW $Z = 0.24$, $P = 0.81$, $n = 66$) or fledging age (MW $Z = 1.64$, $P = 0.10$, $n = 66$) between sexes. The increments in body mass and wing length for male and female nestlings were best described by quadratic regressions (Fig. 3). Male nestlings ($n = 26$) reached a mean asymptotic mass of $99.47 \text{ g} \pm 10.42 \text{ g}$ (range 68.75–114.51 g) at 33.65 ± 5.92 days of age (range 15–48 days). Pre fledging mass for males averaged $92.31 \pm 11.08 \text{ g}$ (range 67.28–106.48 g), which represents a mass recession of $7.16 \pm 5.74 \text{ g}$ (range 0–19.9 g) or $7.18\% \pm 5.76$ (range 0–20.43%) decrease from asymptotic mass. Males fledged at 42.23 ± 3.85 days (range 31–49 days). Female nestlings ($n = 40$) reached a mean asymptotic mass of $92.12 \text{ g} \pm 12.74 \text{ g}$ (range 62.58–132.69 g) at 29.97 ± 5.69 days of age (range 17–42 days). Subsequently, female pre fledging mass averaged $83.56 \pm 10.67 \text{ g}$ (range 54.17–106.4 g), which represents a mass recession of $8.55 \pm 11.13 \text{ g}$ (range 0–61.29 g) or $8.63\% \pm 9.62$ (range 0–46.19%) decrease from asymptotic mass. Females fledged at 40.2 ± 4.62 days (range 31–49 days). Pre fledging wing length of male nestlings ($n = 26$) reached $149.61 \text{ mm} \pm 15.09 \text{ mm}$ (range 118–170 mm) at 41.23 ± 3.85 days of age (range 30–48 days). Pre fledging wing length for female nestlings ($n = 40$) reached $139.45 \text{ mm} \pm 15.67 \text{ mm}$ (range 88–165 mm) at 39.2 ± 4.62 days of age (range 30–48 days).

At the brood level, pre fledging mass, brood size, total hatching asynchrony, mass recession and clutch initiation date were all poor predictors of mean fledging age: pre fledging mass $y = 23.26 + 0.19 * x$; $r^2 = 0.003$, $P = 0.14$; brood size $y = 37.44 + 0.5 * x$; $r^2 = 0.6$, $P = 0.40$; total hatching asynchrony $y = 39.72 + 0.05 * x$; $r^2 = 0.003$, $P = 0.84$; mass recession $y =$

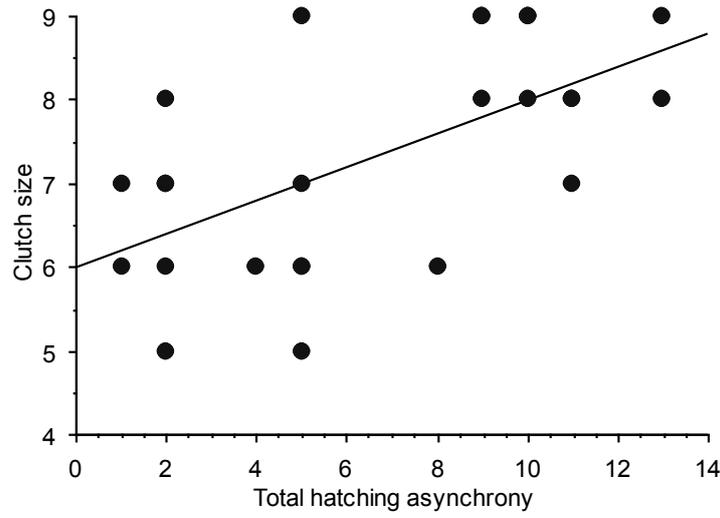


Figure 1. Relationship between clutch size and total hatching asynchrony (time span in days between hatching of first and last egg laid in a clutch) for the red-crowned parakeet. Note that equal-sized clutches hatched over different time spans.

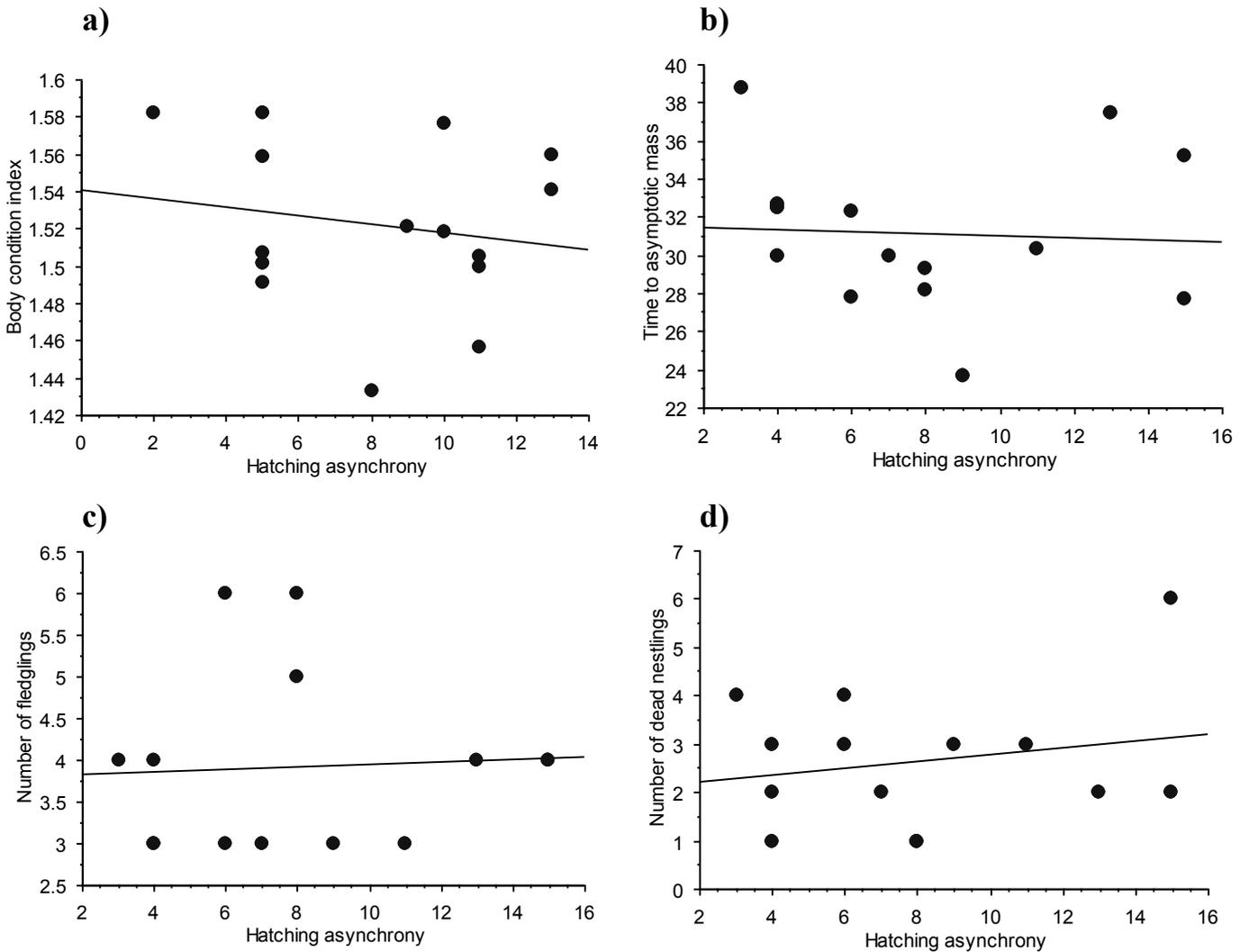


Figure 2. Relationship between hatching asynchrony and body condition index (a); time (in days) to reach asymptotic mass (b); number of fledglings per brood (c) and number of dead nestlings per brood (d) in the red-crowned parakeet.

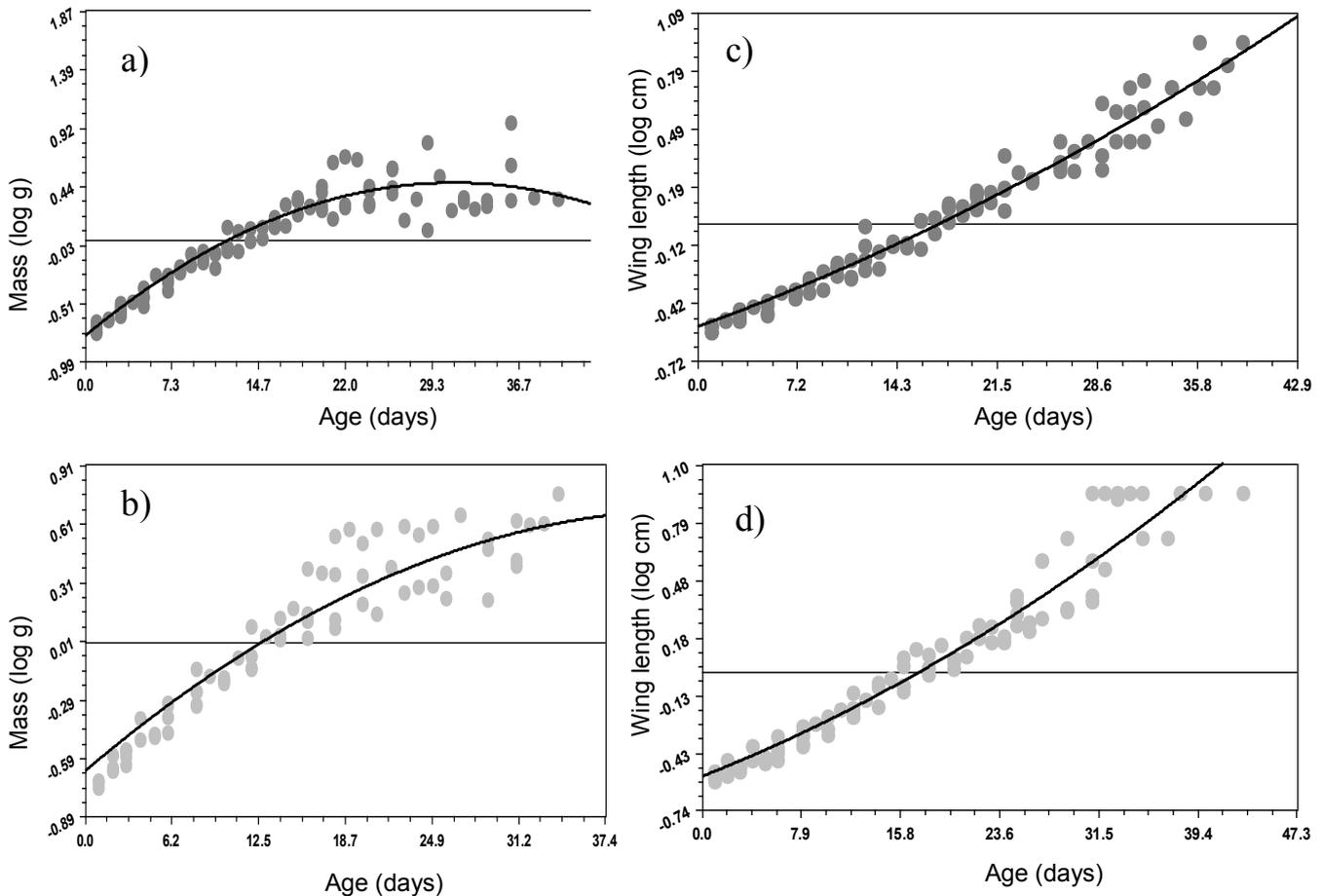


Figure 3. The pattern of growth of female (dark grey) and male (light grey) red-crowned parakeet nestlings: left: a) and b) mass increase; right c) and d): wing growth.

Table 1. Effects of hatching rank on nestling growth. χ^2 refers to Kruskal-Wallis tests. Values are means \pm SE.

Hatching rank	First (n = 19)	Middle (n = 20)	Last (n = 20)	χ^2_2	P
Asymptotic mass (g)	99.20 \pm 2.62	95.88 \pm 2.29	89.25 \pm 3.14	4.21	> 0.12
Final mass (g)	91.59 \pm 2.48	86.74 \pm 2.29	81.89 \pm 3.13	5.32	> 0.06
Asymptotic culmen length (mm)	13.64 \pm 0.33	13.63 \pm 0.25	12.31 \pm 0.33	10.35	< 0.05
Asymptotic tarsus length (mm)	24.71 \pm 0.26	24.64 \pm 0.29	23.94 \pm 0.34	3.48	0.17
Asymptotic wing length (mm)	148.36 \pm 2.37	147.80 \pm 1.91	131.05 \pm 3.65	16.47	0.01

39.13 + 0.11 * x; $r^2 = 0.06$, $P = 0.38$; clutch initiation date $y = 42.07 - 0.06 * x$; $r^2 = 0.08$, $P = 0.33$. Fledglings of the same brood left the nest sequentially and up to 13 days separated fledging of the first chick and the last (duration of fledging period 4.70 ± 2.98 days, range 0–13 days, $n = 22$).

Hatching rank affected skeletal measures among nestlings, with first hatched nestlings tending to have longer culmen and wing lengths than other hatch ranks. (Kruskal-Wallis (KW) test culmen $\chi^2 = 10.35$, $P < 0.01$; wing $\chi^2 = 7.39$, $P < 0.01$). Final mass and asymptotic mass did not differ significantly between hatch ranks (KW final mass $\chi^2_2 = 5.32$, $P = 0.06$; KW test asymptotic mass $\chi^2 = 4.21$, $P = 0.12$).

Clutch initiation date was negatively related to body condition, with earlier laid clutches resulting in broods of higher mean body condition index; this relationship was significant (linear regression $r^2 = 0.31$, $F = 5.42$, $P = 0.04$, $n =$

14) (Fig. 4). Clutch initiation date was significantly correlated with brood size, with earlier laid clutches resulting in more nestlings per brood (linear regression $r^2 = 0.09$, $F = 4.68$, $P = 0.04$, $n = 47$) (Fig. 4); in turn, larger broods yielded more fledglings (linear regression $r^2 = 0.39$, $F = 28.80$, $P < 0.001$, $n = 47$) (Fig. 4). Finally, the number of dead nestlings was positively correlated with brood size; larger broods having more dead nestlings (linear regression $r^2 = 0.36$, $F = 25.72$, $P < 0.001$, $n = 47$) (Fig. 4).

During our study, 44 nestlings from 24 broods died. Every dead nestling had an empty crop indicating starvation was the cause of death. Mortality was significantly more frequent for last hatched nestlings than for other hatch ranks (proportion of dead nestlings: first hatched 10%; middle hatched 21%; last hatched 68%; $\chi^2 = 13.82$, $P < 0.01$). The mean age at death was 14.37 ± 10.89 days (range 1–46 days, $n = 44$). For

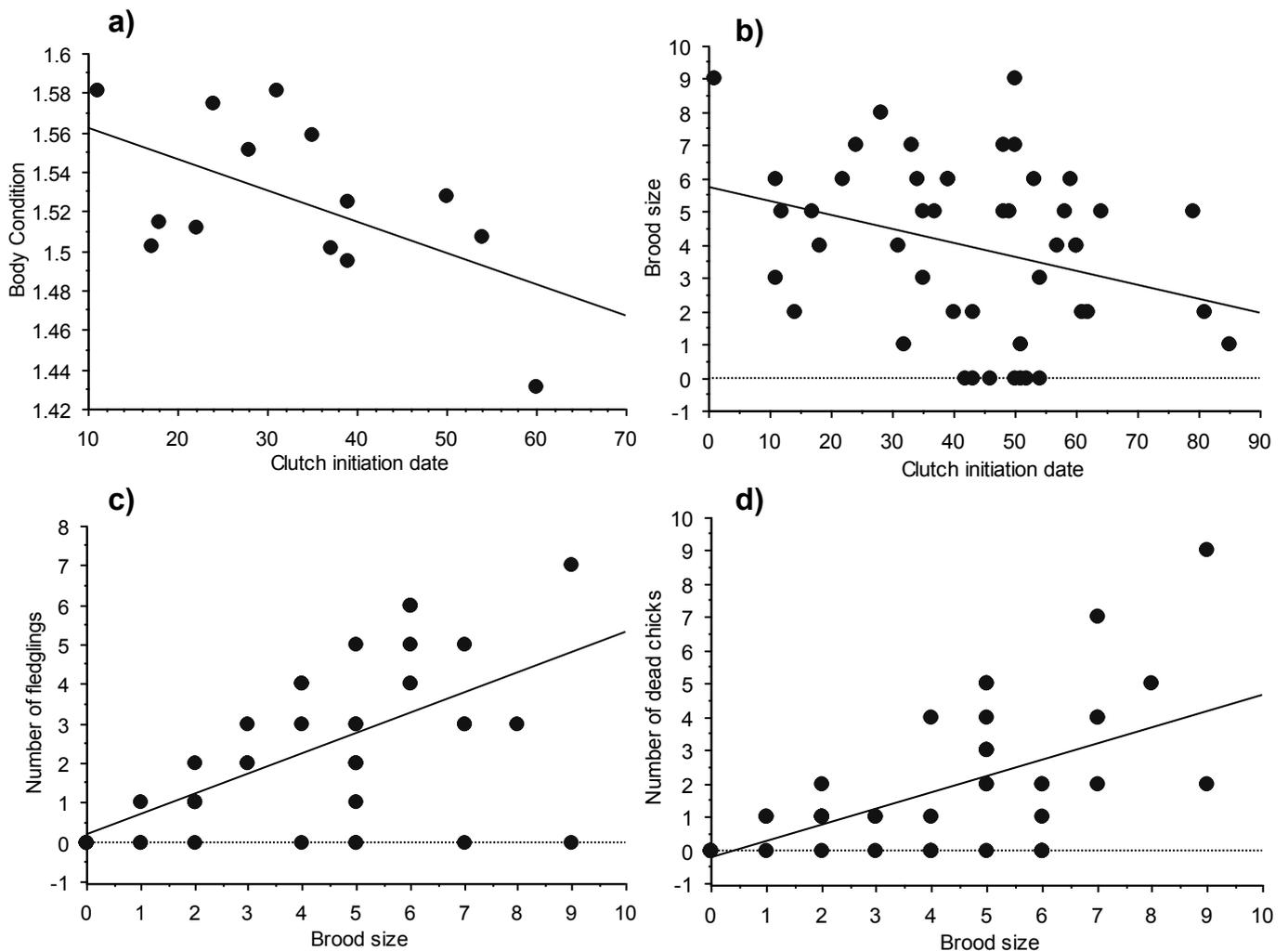


Figure 4. Top: relationship between clutch initiation date and body condition index (a) and brood size (b). Bottom: relationship between brood size and number of fledglings (c) and number of dead nestlings per brood (d).

nestlings that could be sexed after death, the proportion that were females was 42%. This did not differ significantly from 50% (binomial test $Z = 0.49$, $P = 0.32$, $n = 19$ nestlings from nine broods).

The primary sex ratio in 16 broods was 50.5%:49.5% (females: males) and did not differ significantly from parity (binomial test $Z = 0.10$, $P = 0.92$, $n = 95$ embryos/chicks). Similarly, the proportion of females in 18 broods at hatching (59.5%) was not statistically different from that of males (40.5%; binomial test sex ratio at hatching $Z = 1.62$, $P = 0.10$, $n = 82$ hatchlings). Finally, the fledging sex ratio in 22 broods was 60.6%:39.5% (females: males), but not statistically different from parity (binomial test sex ratio at fledging $Z = 1.72$, $P = 0.08$, $n = 66$ fledglings).

Discussion

Our results indicate that in the absence of nest predation by introduced mammals, negative correlations of clutch initiation date with clutch size and, in turn, seasonally-invariable starvation-driven brood reduction are the most important factors determining survival of red-crowned parakeet nestlings. From our statistical analyses, it appears the degree

of hatching asynchrony is insufficient to explain variability in body condition indices among nestlings and number of dead nestlings within broods. Psittaciform clutches hatch with variable degrees of asynchrony and, as a rule, the survival of parrot nestlings is closely related to hatching rank and degree of hatching asynchrony, based on field (Masello & Quilfeldt 2002) and experimental studies (Stolesson & Beissinger 1997). In contrast, a relative of red-crowned parakeets in the subfamily Platycercinae, the crimson rosella (*Platycercus elegans*) raises asynchronous broods to similar mass and size ranges of synchronous broods (Krebs 1999). However, nestling mortality in crimson rosella is still higher for last hatched nestlings (Krebs 1999). Our findings from the red-crowned parakeet suggest that breeding pairs are able to compensate for asynchrony and the resulting size hierarchies among nest mates, and successfully fledge young within average values of body condition. The mortality of nestlings in our study was more frequent among last hatching nestlings, in accordance with most research on asynchronously hatching altricial bird species (Magrath 1990; Beissinger & Stolesson 1997).

Fledging age of red-crowned parakeets was highly variable and unrelated to pre-fledging mass, brood size, total hatching asynchrony, mass recession or clutch initiation date. Pre-fledging mass recession and fledging age in birds are the

outcome of behavioural and energetic interactions between parents and nestlings (Gray & Hamer 2001; Gjerdrum 2004), with the added effects of predation risk at the nest (Harfenist & Ydenberg 1995). Like the colonial-breeder burrowing parrot (*Cyanoliseus patagonus*) (Masello & Quilfeldt 2002), red-crowned parakeets on Tiritiri Matangi, free of mammalian exotics, did not suffer predation during the nesting period either in artificial nest boxes or in natural cavities. Further, nest type on Tiritiri Matangi does not affect nesting success for red-crowned parakeets (Ortiz-Catedral & Brunton 2009). Thus, behavioural responses to predation pressure or nest type might be irrelevant to explain timing of fledging. Accordingly, during our data collection we often noticed very young and near-fledging stage nestlings sitting right at the entrance of the nest or within a few centimetres of the entrance in the case of ground nests. Moreover, nestlings seemed unaffected by the researcher's presence in the vicinity of the nest and would only retreat inside when researchers attempted to capture them for measurements and sampling.

In red-crowned parakeets, the lack of biases in primary sex ratio and sex ratios at hatching and fledging could be related to a similar reproductive value of males and females. In the crimson rosella, males and females differ in their age at first breeding and a significant association between egg laying date and a sex ratio bias towards females has been reported (Krebs et al. 2002). Alternatively, our sample size might have been too small to detect small biological biases in sex ratios, although statistically our study was above the recommended threshold (Ewen et al. 2004; Ismar et al. 2010). Although there have not been specific studies in any *Cyanoramphus* parakeets to determine the age at first breeding, field observations on Malherbe's parakeets (*C. malherbi*) indicate that juveniles can pair up at 7 months of age (Ortiz-Catedral et al. 2009b). There is also one record of a female red-crowned parakeet pairing up within weeks of fledging (Greene 2003), suggesting that early pairing up by both sexes and possibly breeding is likely in this species also.

Overall, our research has important implications for understanding the biology and conservation management of *Cyanoramphus* parakeets which have been translocated to various predator-controlled and predator-eradicated locations within New Zealand (McHalick 1999; Ortiz-Catedral & Brunton 2010). There have also been recent suggestions to reintroduce them to Lord Howe Island from a remnant population on Norfolk Island (Hutton et al. 2007) and the potential of using captive-bred individuals for reintroduction has long been discussed for this genus, in particular for the red-crowned parakeet (Dawe 1979; MacMillan 1990; Grant & Kearvell 2001; Ortiz-Catedral et al. 2009b). Red-crowned parakeets in our studies showed marked variability in clutch parameters and nesting success between breeding seasons (Ortiz-Catedral & Brunton 2008; Ortiz-Catedral & Brunton 2009; this report), and we have observed here that the timing of clutch initiation and the overall hatching asynchrony of the broods are both related to the condition and productivity of broods (see results). Consequently, we recommend close monitoring of the timing of breeding of potential source populations prior to capturing individuals for translocations, and for the estimation of the impact of breeding productivity on the structure and size of populations. Understanding the basic biology and monitoring breeding dynamics are necessary to predict the brood productivity of red-crowned parakeets in a target breeding season, to maximise the efficiency of conservation funds available for the translocation of this, and likely other, related native parakeets.

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