Ararajuba 4(2):81-85
dezembro de 1996

Nestling development, size and juvenile survival in *Donacobius atricapillus* (Passeriformes: Troglodytidae)

José Ragusa-Netto[1]
Departamento de Zoologia UNESP, C.P. 199, 13506-900, Rio Claro, SP, Brazil

Recebido em 12 de agosto de 1996; aceito em 07 de novembro de 1996

RESUMO. Desenvolvimento dos ninhegos e sobrevivência dos jovens em *Donacobius atricapillus* (Passeriformes: Troglodytidae). *Donacobius atricapillus* caracteriza-se por apresentar reprodução cooperativa, viver e nidificar em brejos. Neste estudo avaliei o desenvolvimento dos ninhegos de *D. atricapillus*, e o impacto da massa corporal, 15 dias após a eclosão dos ovos, na sobrevivência pós-ninho. A massa dos ninhegos no dia 15 variou de 20,0 a 32,0 g ($\bar{x} \pm$ dp; 26,7 ± 2,7 g; N = 82). As ninhadas foram constituidas por 2 ou 3 ninhegos, atendidos por 2 ou 3 adultos. A eclosão foi menos assincrônica em ninhadas com 2 ninhegos, cuja massa média no dia 15 foi de 27,5 ± 3,1 g (N = 34). Nas ninhadas maiores, mais assincrônicas, a massa média foi significativamente menor (26,2 ± 5,4 g; N = 48; ANOVA, duas variáveis de classificação, F = 3,71; p < 0,05). O número de adultos atendendo os ninhos não apresentou relação com a massa dos ninhegos. No entanto, ninhos atendidos por 3 adultos foram mais produtivos (χ^2 = 12,11; p < 0,05). Do conjunto de ninhegos (N = 72) que deixaram os ninhos, verifiquei que a massa no dia 15 correlacionou-se significativamente com a sobrevivência pós-ninho (coeficiente de correlação de Spearman, r = 0,90; p < 0,05; N = 5). Com o propósito de minimizar o efeito do número de adultos sobre a sobrevivência, a massa dos ninhegos foi avaliada em relação à dos demais parceiros de ninho. Com isto, verifiquei que apenas 4 de 17 jovens apresentavam, quando ninhegos, massa inferior à dos irmãos (χ^2 = 4,76; p < 0,05). Estes resultados reafirmam as baixas chances de sobrevivência dos ninhegos menores. Além disso, os resultados indicam que a presença de auxiliares aumentam as chances de sobrevivência pós-ninho.
PALAVRAS-CHAVE: aves, *Donacobius atricapillus*, ninhegos, reprodução cooperativa, sobrevivência juvenil, tamanho das ninhadas.

ABSTRACT. *Donacobius atricapillus* is a cooperatively breeding marsh-living bird. I examined nestling development and the impact of nestling size on juvenile survival. Nestling mass at day 15 ranged from 20.0 to 32.0 g ($\bar{x} \pm$ sd; 26.7 ± 2.7 g; N = 82). In nests, 2 or 3 nestlings developed, reared by 2 or 3 adults. Hatching was less asynchronous in broods of 2 nestlings, which achieved a higher mean mass (27.5 ± 3.1 g, N = 34) at day 15, in relation to nestlings in broods of 3 (26.2 ± 5.4 g, N = 48, two-way ANOVA, F = 3.71, p < 0.05). The number of adults attending had no effect on nestling mass. However, nests attended by 3 adults were more productive (χ^2 = 12.11; p < 0.05), as a result of better survival during the month after fledging. Nestling mass Day 15 (N = 72) were significatively correlated with juvenile survival 30 days after fledging (Spearman's rank correlation coefficient, r = 0.90, p < 0.05, N = 5). For the purpose of removing the effect of adult number on juvenile survival, a within-brood analysis was employed. Only 4 of 17 surviving juveniles were lighter than their nest mates (χ^2 = 4.76; p < 0.05). As in other studies, small nestling survive less well, whereas presence of a helper seems to aid post-fledging survival.

KEY WORDS: brood size, cooperative breeding, *Donacobius atricapillus*, juvenile survival, nestlings, nestling mass.

Nestling growth may be affected by such factors as environmental conditions, parental experience, territory quality, brood size and hatching synchrony (for a review, see Ricklefs 1983). The effect of nestling size on juvenile survival up to acquisition of nutritional independence has been the subject of some studies (Martin 1987), partly because of the difficulties of monitoring broods after fledging (but see Sullivan 1989, Magrath 1991).

The Black-Capped Donacobius (*Donacobius atricapillus*) is a territorial, marsh-living species with cooperative breeding. Young stay in the natal territory with parents at least until the next breeding season (Kiltie and Fitzpatrick 1983). In cooperatively breeding birds, survival of young may result from better feeding or from protection by several adults (reviewed in Brown 1987, Stacey and Koenig 1990). If the masses of nestlings that

[1] Present address: Departamento de Ciências do Ambiente, CEUC, C.P. 252, Av. Rio Branco, 1270, UFMS, 79304-020, Corumbá, MS, Brazil

survive are compared to the average mass of nest mates, the effect of adult number in rearing can be minimized (Mumme 1992). In this way, it is possible to evaluate more precisely the consequences of nestling size on young survival. In this study, I examined nestling development and juvenile survival in *D. atricapillus* in relation to brood size, and number of attending adults.

STUDY SITE AND METHODS

Field studies were conducted near Cerquilho (São Paulo State), in marshes (length 5.6 Km, 40-200 m in wide) on two ranches, Mato Dentro (23°11'S, 47°41' W, altitude 508 m) and São Pedro (23°13'S, 47°45' W, altitude 532 m). Grasses and *Typha* sp. are the dominant vegetation. In the breeding seasons of 1989-1990 and 1990-1991, I studied breeding biology in *D. atricapillus*. Nest building starts with heavy rainfall in October. I visited each site at least every 3 days, to find nests and study nestling development. Observations lasted from 06:00 to 10:00, when the chances of visual contact with birds were maximal. Nests found before the first egg were revisited 17-18 days after the last egg was laid [incubation and nestling phases are 16-18 days each: Kiltie and Fitzpatrick (1983)]. Nests found with eggs were visited every two days up to hatching. The masses of nestlings were taken daily, between 12:00 and 14:00. I used a 50-g Pesola spring balance for measurements, which extended up to Day 15 (hatching = Day 0). At this time a plateau in nestling mass was evident (see results), so nestling mass on Day 15 was used for analysis of relationships between nestling size and juvenile survival. Adults strongly defended nests while I handled nestlings, coming within 1 m. Using this response, I determined the exact number of adults at a given nest. For initial identification, nestlings were marked with non-toxic paint. From Day 10, a pair of color rings enabled recognition. To confirm successfull fledging, nests were visited again on Day 17.

Juveniles feed themselves 30 days after leaving the nest. At this time, I visited study sites daily between 06:00 and 10:00 to check juvenile survival.

Statistical procedures follow Sokal and Rohlf (1981), and Zar (1984).

RESULTS

In the two breeding seasons, I found 74 nests in which two or three eggs were laid. I evaluated the possibility of correlation between clutch size and adult number at the nest. From 53 nests found before the first egg (this sample was used to avoid bias caused by the possibility of partial nest predation and/or egg removal), I verified that the proportion of 3-egg clutches was almost the same for nests attended by two (22 of 36 nests) or three adults (11 of 17).

In 33 nests, 82 nestlings were measured from hatching to Day 15. In the two following days 10 nestlings were lost, two by drowning below the nest. Eight (in three broods) were depredated, judging by feathers left in the nest. Broods had two or three nestlings (N = 17 and N = 16, respectively), with 10 broods of two nestlings attended by two adults, and seven by three adults; 13 broods of three nestlings were attended by two adults, and three broods by three adults.

Nestling mass at day 15 ranged from 20.0 to 32.0 g, with average ($\bar{x}$ ± sd) mass 26.7 ± 2.7 g. A two-way ANOVA was employed to evaluate the effects of brood size and adult number attending nests, over nestling mass at Day 15. Adult number had no effect ($F = 0.057$, n.s.). On the other hand, brood size had a significant effect on nestling mass (mean mass 27.5 ± 3.1 g in broods of 2 and 26.2 ± 5.4 g in broods of 3, $F = 3.71$, $p < 0.05$, figure 1). Figure 2 illustrates nestling growth curves in the two kinds of broods. Nestlings were larger in broods of two by about day three.

Hatching was more asynchronous in the 3-egg clutches, where the time span between hatching of the first and third egg reached 30 h. In these broods a nestling mass hierarchy was evident in every nestling growth phase (for nestling mass Day 15, first-hatched nestling = 28.0 ± 1.9g and last-hatched nestling = 25.0 ± 2.3 g, ANOVA, $F = 4.80$; $p < 0.05$). In smaller broods, nestlings did not show significant differences in mass (first-hatched nestling = 27.7 ± 3.0 g; last-hatched nestling = 27.1 ± 3,3 g, paired t test, $t = 0.51$, n.s.; one tail, figure 3).

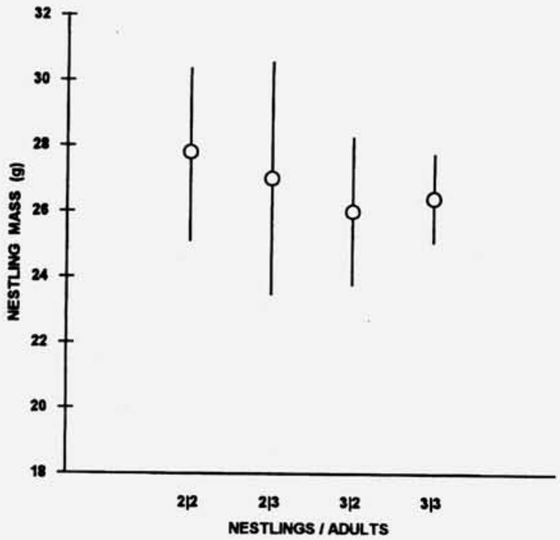

Figure 1. Nestling mass Day 15 after hatching in the four growth situations. Open circles are the mean, vertical lines standard deviation. 2/2- two nestlings (N = 20) attended by two adults; 2/3- two nestlings (N = 14) attended by three adults; 3/2- three nestlings (N = 39) attended by two adults; 3/3- three nestlings (N = 9) attended by three adults.

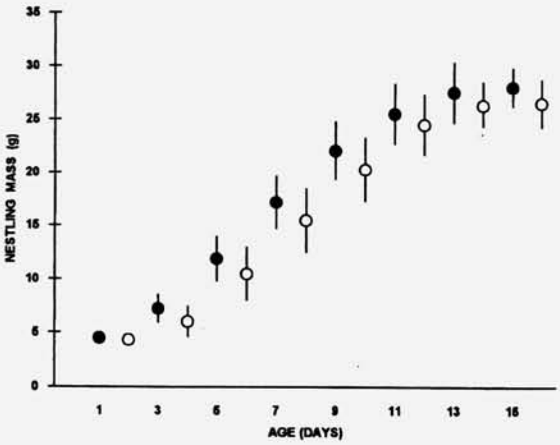

Figure 2. Nestling growth curves in broods of different sizes. Full circles, means for nestlings (N = 34) in broods of 2. Open circles for nestlings (N = 48) in broods of 3. Standard deviations on both sides of mean are also given.

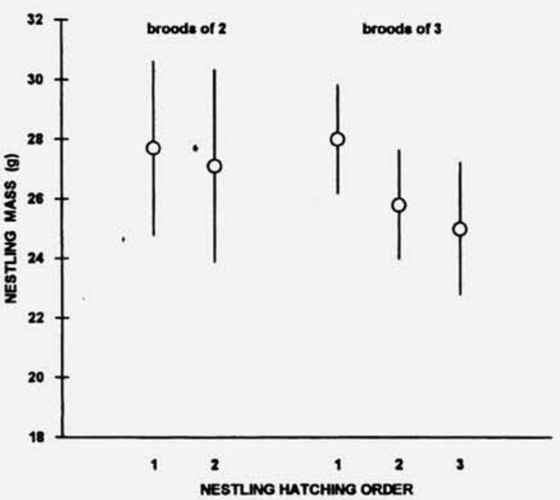

Figure 3. Nestling mass Day 15, following hatching order in broods of 2 and 3 nestlings (N = 34 and N = 48, respectively). Symbols as in figure 1.

A total of 72 nestlings left nests successfully. After fledging, 42 young disappeared before independence. Nestling mass Day 15 were assigned in five classes and checked for the percent of juveniles surviving 30 days after fledging. Thus, I found a significant correlation (Spearman's rank correlation coefficient, $r_s = 0.9$, $p < 0.05$, figure 4). This analysis is a first evidence of the relationship between

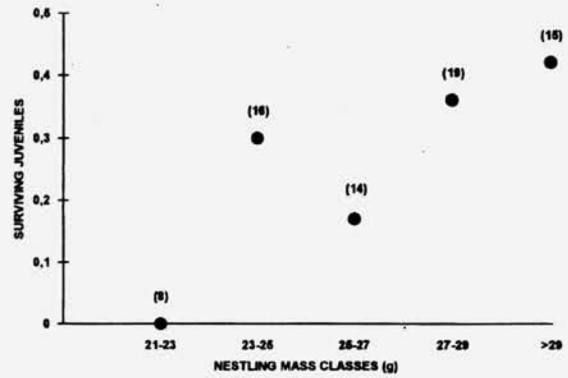

Figure 4. Correlation between nestlings mass Day 15 (in classes) and percent of surviving juveniles 30 days after fledging. In brackets the number of nestlings in each class.

size as nestling and juvenile survival. However, other factors might influence survival independently of the mass as nestling.

Predation rates on nests attended by 2 or 3 adults, as well in broods of 2 or 3 nestlings, were not significantly different (Ragusa-Netto 1994). However, to check if some social factor may have influenced juvenile success, these data were analysed by a 3-way χ^2 (table 1). Juvenile survival was correlated with social factors ($\chi^2 = 10.08$, $p < 0.05$). Brood size was not correlated with juvenile survival ($\chi^2 = 7.26$, $p > 0.10$). Adult number had a significant correlation ($\chi^2 = 12.11$, $p < 0.05$). Because adult number had no effect on nestling mass, some other variable (probably better protection of fledglings when there were three adults in the group) influenced young productivity.

To analyze the influence of nestling mass on juvenile survival independently of the effect of adult number, a within-brood analysis was performed (Mumme 1992). In

Table 1. Surviving juveniles in relation to brood size and number of attending adults.

Brood	Number of attending adults			
	2		3	
size	surviving	disappeared	surviving	disappeared
2	4	12	6	3
3	13	24	7	3

some broods all fledglings (N = 13) survived to independence. These juveniles were excluded from the analysis. I found only four surviving juveniles whose nestling masses were lower. Thus, 13 of 17 survivors had larger masses as nestlings than their nest-mates ($\chi^2 = 4.76$, $p < 0.05$).

DISCUSSION

Nestling mass was related to brood size. Larger broods, more asynchronous, produced on average smaller nestlings. Whatever the selective pressuresthat mantain asynchronous hatching in *D. atricapillus*, one effect was that nestlings were sorted into a hierarchy of size. This probably resulted from more intense food competition (Stouffer and Power 1991). Martin (1987) reviewing this theme, reported studies of natural changes in brood size that have influenced nestling mass. In most cases the larger broods have produced small nestlings. In manipulated broods, (Patterson *et al.* 1980, Nur 1984, Husby 1986, Slagsvold 1986, Stouffer and Power 1991), the smaller broods produced nestlings with higher masses. Crossner (1977) manipulated broods of *Sturnus vulgaris* and food availability in some territories. The enlarged broods in territories with low food availability produced smaller nestlings.

Many studies indicate positive relationships between nestling size and post-fledging survival (Perrins 1965, Perrins *et al.* 1973, Jarvis 1974, Loman 1977, Garnett 1981, Drent 1984, Coulson and Porter 1985, Davies 1986, Gustafsson and Sutherland 1988, Smith*et al.* 1989, Magrath 1991, Mumme 1992). However, these relationships were tested for a small number of species (review by Magrath 1991). The results for *D. atricapillus* are similar to the above-cited results, even thogh *D. atricapillus* differs by being a cooperatively breeding tropical species.

An analysis of survival chances for juveniles, relative to nestlings mass, is necessary before checking other variables that affect juvenile success. Rabenold (1984) found that larger groups of *Campylorhynchus nuchalis* are six times more productive than the small ones. Austad and Rabenold (1985) verified in *Campylorhynchus griseus* a less dramatic difference, although significant, in which breeding pairs plus a helper are three times more productive than unassisted pairs. In these studies, adult numbers attending nests were unrelated to amount of food delivered to nestlings. Instead, large groups provided better protection at nests. Kiltie and Fitzpatrick (1983) verified in *D. atricapillus* a greater production of young when a breeding pair was assisted by helpers. Mumme (1992)experimentally verified higher reproductive success in groups of *Aphelocoma coerulescens* linked to helper presence and activity. Larger groups of these species are correlated with both higher nestling food delivery and to better protection. He also found higher survival by larger nestlings after leaving the nests.

The reasons that larger nestlings are more likely to survive to independence are unclear. As pointed by Magrath (1991) and Mumme (1992), it may be that well-fed and well-developed young acquire critical motor skills more rapidly than poorly-fed and poorly-developed young. Thus, the amount of time in which fledglings are vulnerable to predators is reduced. Well-fed young may beg less frequently and attract fewer predators than undernourished young. Other possibilities are that large young may be better able to survive brief periods of post-fledging food shortage.

All of these hypotheses may be applied to *D. atricapillus*. Their nests are placed in marshes that are flooded in the rainy season, exposing fledglings to the risk of drowning. In addition, predation on nests and fledglings can be severe in the tropics (see reviews, Ricklefs 1969, Skutch 1985). The majority of *D. atricapillus* nests were lost to predation (Ragusa-Netto 1994), making clear the effect of this factor in early phases of development. In this way, well-fed and well-developed young may display skills that enable them to adopt behaviors less risky to predator actions and other environmental threats. Also, an extra adult helping the pair may incrase vigilance for fledglings reducing the risk of predation.

ACKNOWLEDGMENTS

The author is grateful to E. O. Willis for the advice throughout the study, with helpful insights, and the final review of the manuscript. I thank several farmers of Cerquilho, that permited me work on their ranches. Two anonymous reviewers made helpful comments that improved the manuscript. This work was supported with a grant from Brazilian National Research Council (CNPq).

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