REPRODUCTION AND SOCIAL ORGANIZATION OF THE BLACK-CAPPED DONACOBIUS (*DONACOBIUS ATRICAPILLUS*) IN SOUTHEASTERN PERU

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ABSTRACT.—A color-banded population of Black-capped Donacobius (*Donacobius atricapillus*) on a Peruvian oxbow lake was studied during one breeding season and censused for 3 yr thereafter. Eighteen territories along a marshy shoreline were occupied by groups of 2–4 donacobius. Each group contained a mated pair and 0–2 helpers, apparently offspring produced during 1–2 preceding breeding seasons. Helpers participated in nest surveillance, territorial displays, and feeding nestlings. Displays occurred at territory boundaries and consisted of loud duetting by the pair or group. Breeding coincided with the rainy months, October through April, and peaked in November–January. Clutch size was always two. Egg and nestling periods each lasted 17–18 days. No correlation was demonstrable between group size and overall fledging success. Trios, however, accounted for all cases in which both young successfully fledged, whereas pairs never fledged more than one young. Annual survivorship of breeding adults averaged 71%. Cooperative breeding in donacobius is associated with limited opportunities for acquiring breeding territories, as in many other cooperative breeders. The relatively short period during which young serve as helpers (and the resulting small family sizes), however, suggests that at other times or places breeding territories are more readily available to young. *Received 9 November 1983, accepted 19 April 1984.*

THE Black-capped Donacobius (*Donacobius atricapillus*) is distributed widely in lowland tropical South America (Meyer de Schauensee 1970). Little has been published on the behavior and ecology of this aberrant monotypic species, which was recently reclassified as a wren (Troglodytidae) rather than as a mimid (Clench et al. 1982, A.O.U. 1983). Only Skutch (1968) has briefly described the nesting of donacobius in Venezuela. In this paper, we describe the social organization and reproductive attributes of a population of donacobius living along the shore of an oxbow lake in southeastern Peru. With this report, the species joins the ever-growing list of birds exhibiting cooperative breeding.

METHODS AND STUDY SITE

All observations were made on Cocha Cashu (Fig. 1), an oxbow lake about 1 km from the Manu River in the Manu National Park, Dept. Madre de Dios, Peru (71°19'W, 11°51'S), at about 400 m elevation. The lake is surrounded by tall tropical moist forest (Holdridge 1967, see Terborgh et al. 1984 for detailed habitat descriptions and a complete checklist of birds at the site). On the shallower (western) side of the lake, most of the margin is lined with marsh grass and sedge (primarily *Panicum grande* and *Scleria microcarpa*) up to 2 m tall. Other vegetation on this shore includes scattered patches of *Heliconia marginata* up to 5 m tall, occasional figs (*Ficus trigona* and two unidentified species), and, at the extreme northern end, some overhanging limbs of other forest trees. The opposite (eastern) shore has little marsh but, instead, is lined with overhanging limbs of forest trees and vines.

Between July and August 1975, 13 adult-plumaged donacobius were color banded. During August–December 1976, 29 more were banded, so that by January 1977 42 of 46 adult-plumaged donacobius on Cocha Cashu were individually identifiable. Our most detailed observations (≈500 field hours) of reproduction and social organization in the population were made during October 1976–January 1977 and April–June 1977. The population was subsequently censused in August 1978 and September 1979. Casual observations were made in the course of other studies during the May–September dry seasons between 1974 and 1981.

Because donacobius activity was confined to the margins of the lake and the birds were not secretive, censuses could be conducted from a canoe. Reproductive activities could also be monitored from a canoe, because nests were constructed in low grass near the water's edge. During the 1976–1977 breeding season, 15 nests in which eggs were laid were checked at least every other day from the time of their dis-

covery until the nest failed or young fledged. Thir-
teen nestlings were color banded. Territorial bound-
aries were determined by observing the movements
of marked individuals and by mapping locations of
territorial disputes.

Measurements of museum specimens indicate that,
on average, adult male donacobius are significantly
larger than adult females in wing length (85.4 mm
± 1.95 SD vs. 79.1 ± 2.2), tail length (99.3 mm ± 7.8
vs. 88.9 ± 4.4), tarsus length (30.1 mm ± 1.8 vs.
27.8 ± 1.2), and bill length (15.9 mm ± 0.7 vs. 14.9
± 0.8; $P < 0.001$ in all cases by t-test; $n = 18$ females,
19 males). Unfortunately, such differences are not
great enough to allow visual sex determination in the
field. As described by Fuertes (1913), Skutch (1968),
and in this paper, however, calls appear to differ be-
tween male and female. We suspect that calls also
indicate the sex of nonbreeding individuals, al-
though this remains unproven. Three females were
sexed by the presence of brood patches during the
1976–1977 breeding season (only one member of a
pair brooded), and this evidence coincided with our
sex determination by call. Furthermore, of 12 breed-
ing pairs for which sexes were judged by call and
weights were later determined, the weights of the
presumed males exceeded those of the presumed fe-
males in 11 cases, whereas the two weights were equal
in the twelfth. This result, combined with the evi-
dence of sexual dimorphism from museum speci-
mens, supports the utility of the calls in sex deter-
mination. The average weight of breeding males was
53.0 g ± 5.9 and of breeding females was 44.4 g ±
4.2.

Young were considered to have fledged success-
fully when they were observed flying proficiently
with their natal group. Fledglings had lighter brown
upperparts than did the adults, and they had a broad
white superciliary stripe. The darker coloration of
adult upperparts was acquired by the end of the first
year. The superciliary stripe also usually disappeared
by this time, although narrow white post-ocular
stripes persisted in a few breeding adults.

RESULTS

Behavior and spatial organization.—In October
1976, there were 18 donacobius groups, of 2–4
individuals each, occupying contiguous terri-
tories along the shallower lake edge (Fig. 1).
Our observations of reproduction (beyond)
suggested that each group consisted of a breed-
ing pair and their recent young. Territories
served for nesting and foraging but were not
the only areas used for feeding. The birds most
frequently gleaned larvae and adult arthropods
from leaf surfaces in grass, *Heliconia,* and woody
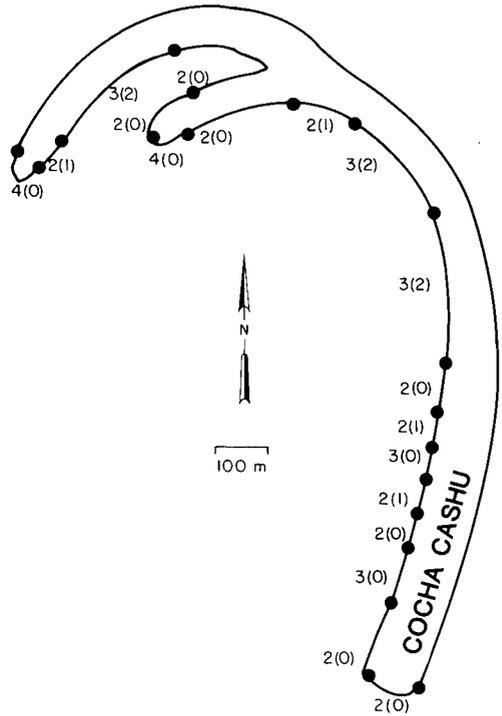thickets along the lakeshore. Adult odonates

Fig. 1. Territories of donacobius groups on the
western, marshy side of Cocha Cashu, 1976–1977. Dots
indicate approximate territorial boundaries. Num-
bers indicate adult-plumaged birds in a group, and
the number of young fledged by each group is in-
dicated in parentheses. (Dimensions of the territories
perpendicular to the lake edge are negligible at this
scale.)

were also hawked from low perches over the
water.

Group members normally foraged within a
few meters of each other. They vigorously dis-
played and called when donacobius who were
not group members entered their area or when
they encountered neighbors at territory
boundaries. During the dry season, it was not
unusual for individual Pale-eyed Blackbirds
(*Agelaius xanthophthalmus*) to forage in close
proximity to donacobius groups, but the black-
birds elicited no defensive donacobius dis-
plays. The Pale-eyed Blackbird has a call simi-
lar to that of donacobius (Parker 1982), and it
nests and forages in the same habitat and sea-
son as donacobius (Kiltie pers. obs.).

As described by Fuertes (1913) and Skutch
(1968), the donacobius display consisted of a
duet by the breeding pair, delivered from ex-

posed perches 2–4 m above the water edge. The male and female typically perched near each other, often side by side. The male uttered a series of ringing, liquid whistles slurred upward, "*whoi-it whoi-it whoi-it*," while his mate emitted a lower, sizzling or grating sound, and the two wagged their fanned-out tails rhythmically from side to side. During active territorial displays, especially frequent during the first 1–2 h after dawn, pairs perched near a shared boundary and alternated duetting bouts with each other. A grating scold, similar to the female's portion of the duet, was made by either sex in response to disturbance or a potential predator. The male's call varied in intensity from slow repetitions of the *whoi-it* whistle (about every 2 s) to rapid bursts of notes when the bird was extremely excited or was responding to playback. Both sexes had bare, bright yellow throat patches, which were inflated and puffed out laterally (especially that of the male) during vigorous calling bouts. Family members other than the breeding pair occasionally joined in the displays. Individual auxiliaries performed only the male or the female portions of the duet; thus, this primary vocalization probably is sex-specific throughout life.

The total lengths of the 18 donacobius territories along the western lake edge ranged from 43 to 282 m ($\bar{x} = 140 \pm 61$ SD). The portions of these territory edges lined only by grass or sedge were less variable (41–155 m; $\bar{x} = 99 \pm 32$ SD). We were unable to measure the dimensions of the territories perpendicular to the lake edge, but territories with small lake-edge distances at the southern end of the lake clearly had greater expanses of marsh and *Heliconia* behind the lake edge than did those with longer lake-edge distances at the north end (Fig. 1). Apparently it is important that a considerable portion of each territory consists of marsh; the territory with the lowest ratio of marshy edge to total lake edge (43 m : 282 m) was abandoned after unsuccessful nesting in 1977 and was not reoccupied for at least 2 yr thereafter. No other territories were vacated during this time.

Donacobius activity was not completely limited to the marshy side of the lake. Groups or individuals occasionally foraged on the opposite lake shore, where they roamed along much greater distances than when on the marshy side. Intergroup aggression and display also occurred on the forested side when the groups met. The locations of these disputes, however, were not as fixed as were the boundaries on the marshy lake margin.

After the breeding season, auxiliary members of groups were frequently seen alone on both sides of the lake, far from their known or presumed natal territories. Auxiliaries were vigorously chased when they entered the territories of other groups. Because wandering individuals were usually seen later in their natal territories, they were probably engaging in "dispersal forays," a trait also exhibited by nonbreeding Florida Scrub Jay (*Aphelocoma coerulescens*) helpers (Woolfenden and Fitzpatrick 1978, in press).

Survivorship, disappearance, and social turnover.—Figure 2 illustrates the proportions of banded donacobius present along the lake shore during three census periods after banding was ended in December 1976. For convenience, these proportions are called "survivorship," although some loss could be the result of dispersal from the lake rather than mortality. We differentiated among (1) donacobius banded as nestlings, (2) breeding individuals banded at unknown age, and (3) adult-plumaged auxiliaries banded at unknown age. The data for breeding adults tightly fit the linear regression model $\log_{10}$ ("survivorship") = 0.0125·(months since December 1976); $R^2 = 0.99$. This straight-line fit indicates a constant survival rate (e.g. see Pianka 1974) of 97% per month, or 71% per year. This rate apparently has persisted beyond our study period. Scott K. Robinson (pers. comm.) reported that six color-banded adults from our study (14% of the original population) still occupied territories in early 1982. The extension of the regression for breeders in Fig. 2 would have predicted that 18% of the original population would be present after this time period (95% prediction interval = 13–25%). We strongly suspect that all loss of breeding adults was the result of mortality; age-independent survivorship is typical among passerine birds (Ricklefs 1973), and there was no evidence of breeders moving after territory acquisition.

Yearly survivorship averaged 44% for banded nestlings and 59% for those banded as auxiliaries. Tests for heterogeneity of slopes (Freund and Littell 1981) among the regressions of $\log_{10}$ (survivorship) vs. time indicated that average survivorship of banded nestlings differed significantly from that of breeding adults ($P = 0.036$), but that the survivorship of
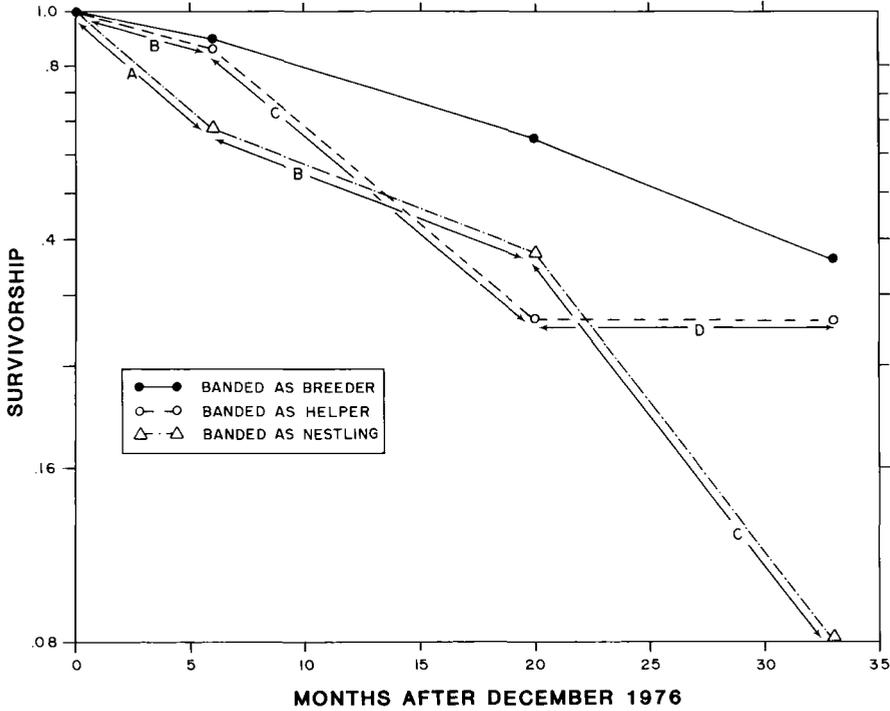
Fig. 2. Proportionate survivorship of donacobius at three censuses up to 33 months after banding of breeding adults (original $n = 42$), helpers (original $n = 13$), and nestlings (original $n = 7$) in November–December 1976. Note logarithmic ordinate scale. Different line segments for helpers and nestlings correspond to the following life stages: A. nestling; B. helper in natal group; C. dispersal; D. establishment in breeding territory.

birds banded as auxiliaries did not differ significantly from that of breeding adults or of birds banded as nestlings ($P = 0.371$ and 0.174, respectively). Nestlings appear to suffer relatively high mortality just before and after fledging. Once fledged, survival is high until dispersal from the natal group. The data for adult-plumaged auxiliaries banded at unknown age suggest a similar pattern: lower mortality while with the natal group, higher mortality at dispersal, and lower mortality for those acquiring breeding territories.

In addition to mortality, dispersal from the lake may account for the loss of some nonbreeding individuals. Aerial photos indicate that other oxbow lakes occur every 1–10 km along the lower reaches of the Manu, from the region of Cocha Cashu to the river's confluence with the Río Madre de Dios. The oxbow closest to Cocha Cashu, about 2 km away, also has a population of donacobius. Transient donacobi-

us have been seen rarely on the banks of the Río Manu. No donacobius has ever been recorded in the forest separating Cocha Cashu from the nearest lake and the Río Manu, nor has a bird banded on Cocha Cashu been sighted on the neighboring oxbow, despite intensive ornithological research and mist-netting in the area (about 4 km²) since 1973 (Terborgh et al. 1984).

In all cases where one member of a banded breeding pair disappeared, the survivor remained on its territory (regardless of apparent sex) and obtained a new mate. During our study, six banded helpers became established in territories different from those in which they had been banded. In two cases dispersal was to an adjacent territory. In a third case, dispersal was from one end of the lake to the other. The remaining three moved intermediate distances.

In three cases of mate replacement, an auxiliary had been present before the breeder's

TABLE 1. Fates of 15 nests in which eggs were laid by 12 donacobius groups (3 renests) at Cocha Cashu, October 1976–April 1977.

Fate of nest contents	Family size		
	2	3	4
Unsuccessful[a]			
2 eggs lost	3	1	1
2 nestlings lost	3	0	0
Successful			
1 nestling lost, 1 fledgling	2	0	0
1 egg or nestling lost, 1 fledgling	2	0	0
2 fledglings	0	3	0
Total samples	10	4	1

[a] Losses of nest contents apparently were caused by predation; no evidence of starvation or disease was noted.

death. In each case, these auxiliaries either disappeared or became breeders elsewhere during the period over which the change in mates was noted. We do not know whether or not these departures were caused directly by the arrival of a new (and less closely related) breeder in the territories. This possibility is suggested, however, by the observation that in none of these cases did the departure of the auxiliary coincide with the fledging of new young. In all seven cases in which banded auxiliaries left a family while both breeders remained on the territory, the departure of the auxiliaries occurred over the period during which new young were fledged. It would appear that helpers are "encouraged" to leave a natal group either by the fledging of a subsequent brood or the loss of one of their parents and the arrival of a "step-parent."

Reproduction and helping.—Nesting behavior (construction of at least partial nests) was seen in all donacobius groups during the 1976–1977 breeding season, but only 12 of the 18 groups definitely produced eggs. Three of these groups (2 pairs and a trio) renested and produced eggs after the loss of the first clutch. Nesting began at the start of the rainy season in October. Of 7 successful nests (those fledging at least 1 young), 5 resulted in fledging between November and January and 2 between February and April. There were no signs of renesting by a pair in a breeding season after they had successfully fledged young. No breeding activity was noted during the dry seasons.

Nests were cup-shaped and were about 10–15 cm in length and width. They consisted of straw woven around several sturdy grass, sedge, or *Heliconia* stems. They were constructed 0.25–1.0 m above water level and up to about 1 m from the edge of the open lake water. Every completed nest contained shed reptile skin (mostly from snakes) incorporated into its structure. Clutch size was two in all cases. Eggs were mottled with various shades of reddish brown, as Skutch (1968) described, and were laid one day apart. They averaged 24.8 mm ± 1.5 long and 17.3 mm ± 1.0 wide at the widest point ($n = 12$). Average egg weight was 3.8 g ± 0.4 ($n = 10$). Incubation lasted 17–18 days, with only the breeding female incubating. Nestlings averaged 4.2 g ± 0.8 on the day of hatching and were 35–40 g on day 12 after hatching. Fledging occurred 16–18 days after hatching.

Table 1 is a list of the fates of the 15 nests in which eggs were found. The loss of nest contents occurred in both the incubation and nestling stages and was presumed to be caused by snake or avian predation. The families successfully fledging young consisted of four pairs (each of which fledged one young) and three trios (each fledging two young). No correlation exists between group size and overall production of young. Successful trios fledged significantly more young, however, than did successful pairs (Fisher exact test, $P < 0.05$).

No observations were made of other individuals feeding the incubating female, but all group members brought food to the nestlings. Judging sex on the basis of calls, we determined that one successful trio included a male helper and one a female helper; the sex of the helper in the third successful trio was not determined. Food items brought to the young included adult odonates, orthopterans, spiders, caterpillars, and other immature insects. All family members participated in surveillance and scolding around the nest when an observer approached their territory.

DISCUSSION

Taxonomic implications.—Our observations of the behavior of donacobius are not taxonomically conclusive but are consistent with the hypothesis that the species is a wren, not a mimid. Three behavioral characteristics independently suggest relationships with the Troglodytidae.

(1) Although the Mimidae and the Troglodytidae both contain cooperatively breeding species, cooperative breeding in the Mimidae, to our knowledge, is limited to certain tropical members of the genus *Mimus* and the closely related *Nesomimus* (e.g. Kinniard and Grant 1982). In contrast, although the extent to which many tropical wrens breed cooperatively still is unknown, the trait is widespread in the genus *Campylorhynchus* (e.g. Rabenold 1984) and appears to occur also in *Thryothorus, Cinnecerthia,* and *Cyphorhinus.*

(2) Vocal and display behavior among mated pairs of donacobius are unlike any we have observed in the Mimidae but are strongly reminiscent of *Campylorhynchus* wrens. Complicated vocal duetting by members of a pair stationed close to each other is commonplace in the latter genus. Usually, these duets are given in response to similar duets by a rival pair near territorial boundaries (Wiley and Wiley 1977). These traits also typify the duetting behavior of donacobius pairs. Both genera incorporate loud, liquid, ringing notes, uttered in rapid sucession, into their songs. Tail-wagging displays similar to the highly stereotyped, lateral fanning motions performed by duetting donacobius also are performed by certain species of *Campylorhynchus.* We are not aware of any such display among mimids.

(3) Donacobius mostly forage in dense shrubs, thick vine tangles, and wet grassy marshes, where they probe and pluck insects from vegetation. They do not dig, probe, or scratch into the ground or litter as do most mimids. As a perching, arboreal species, rather than a terrestrial forager, donacobius ecologically resembles most wrens, especially members of the genus *Campylorhynchus.*

Reproductive ecology.—Skutch's (1968) observations were limited to one nest lacking helpers. His descriptions of territory size, nest construction (including the use of reptile skin), egg size and color, and incubation and nestling periods are all consistent with our observations. One difference is that he found a clutch of 3, whereas we never found more than 2 eggs in a nest.

The donacobius of Cocha Cashu exhibit the most common form of cooperative breeding among birds (Brown 1978): nonbreeders remain in their natal territory up to several years after fledging and help their parents raise subsequent offspring. The ecological constraints

under which this population lives are shared by numerous other cooperative-breeding birds (Emlen 1978, 1982; Koenig and Pitelka 1981; Woolfenden and Fitzpatrick in press): suitable habitat is limited in extent, well-bounded, and relatively homogeneous. It is divided into contiguous, all-purpose territories occupied year-round, and population density is relatively stable. In the case of donacobius, an elaborate and conspicuous communal display accompanies territorial announcement and defense.

At Cocha Cashu and, presumably, throughout much of the lowland neotropics, opportunities for young donacobius to breed at sites other than the natal locale must be rare. Most breeding vacancies probably are filled from within the population. A young, nonbreeding donacobius could improve its chance of eventually gaining its own breeding territory by (1) minimizing its mortality risk early in life, (2) monitoring the breeding population closely to identify any vacancies that occur, and (3) doing what it can to increase the probability that a breeding vacancy will occur (Woolfenden and Fitzpatrick in press). Dwelling in a group within the natal territory undoubtedly contributes to the first of these goals by affording cooperative predator detection and providing familiar foraging places and refuge sites while the young donacobius gains experience. Dispersal forays serve the second function, as a failure to be challenged in another territory would immediately signal that a resident breeder was absent. Annual breeder mortality of about 29% is slightly higher than that reported for other cooperative breeders (Brown 1978) and undoubtedly contributes to the relatively small family groups of donacobius and early dispersal of helpers. We have no evidence that the third goal is served by helpers' raising additional family members, as in Florida Scrub Jays (Woolfenden and Fitzpatrick 1978, in press), or by any other activity.

Because losses of eggs and young from the nests of pairs apparently resulted from predation, the greater success of trios in fledging two young may have been caused by the improved detection and deterrence of predators among the larger groups, as has been shown for Florida Scrub Jays (Woolfenden and Fitzpatrick in press). In 1978, however, presence of unbanded juveniles in territories with banded parents indicated that at least 5 unassisted pairs had successfully fledged 2 young each and 4 had

fledged at least 1 young. Thus, the high loss of young from nests of pairs in 1976 is not necessarily typical. It might be attributed to observer interference, although Lennington's (1979) literature survey indicated that there were significant negative effects of study on blackbird reproduction in marshes only in the second year of such work. In any case, our observations for both years suggest that any effect of helpers upon reproductive success is probably small and perhaps is limited to years of lower overall productivity.

Although successful dispersal to other lakes must be rare, it clearly occurs. New oxbow lakes and other marshy areas are produced by the meandering Río Manu and other rivers like it. No precise estimates are available for the rate at which oxbow lakes are formed, although Foster (1980) suggests that a given point on the floodplain of tropical meander rivers is eroded by the river every 100–1,000 yr. Once formed, oxbow lakes probably last over a similar range of time before being filled by secondary succession (Terborgh 1983). Any pair of donacobius that first colonized an isolated new lake and could breed with reduced competition would undoubtedly leave many more direct descendants than would pairs that breed on lakes with long-established populations. A theoretically intriguing, but empirically daunting, topic for further investigation would be the conditions under which young donacobius "decide" to disperse from their natal population in search of suitable new habitats. Because of the infrequency of new lakes, such a decision would seemingly entail a huge risk, but there would also be a huge potential benefit.

The colonization of new breeding sites would result in a temporary release from some of the ecological constraints mentioned before that are typically associated with cooperative breeding. New colonization would provide an opportunity for the early establishment of yearling breeders. Possibly, then, the social system of the Black-capped Donacobius may be more flexible than that of many other cooperative breeders. Such variability is known in at least two other cooperative breeders, the Pied Kingfisher (*Ceryle rudis*) and the Acorn Woodpecker (*Melanerpes formicivorus*) (Reyer 1980, Emlen 1982). Thus, donacobius may provide a test for the importance of habitat saturation in the evolution of cooperative breeding among birds

(data and models recently reviewed by Woolfenden and Fitzpatrick in press).

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