The Wilson Journal of Ornithology 122(1):46–50, 2010

COOPERATIVE BREEDING OF THE SOCIETY KINGFISHER (*TODIRAMPHUS VENERATUS*)

DYLAN C. KESLER,[1,3] THOMAS GHESTEMME,[2] EMMANUELLE PORTIER,[2] AND ANNE GOUNI[2]

ABSTRACT.—We present evidence of cooperative breeding in Society Kingfishers (*Todiramphus veneratus*). Groups of three kingfishers were observed cooperatively excavating nest cavities, incubating, and provisioning young. Three bird groups also comprised half of visual observations recorded during island-wide point transect surveys that occurred during the onset of breeding. Society Kingfisher densities were an order of magnitude greater than other Pacific kingfisher populations, which may lead to resource saturation and evolution of cooperation in this species. Our results lend insight into cooperative behaviors and facilitate conservation of birds in French Polynesia. *Received 30 July 2009. Accepted 12 October 2009.*

Cooperative breeding has been a focus of behavioral ecologists and evolutionary biologists for decades (Skutch 1935, Brown 1987, Stacey and Koenig 1990, Koenig and Dickinson 2004). Broadly defined, cooperation occurs when more than two individuals contribute to a single brood (Cockburn 2004, 2006). A range of social structures are considered to be cooperative (e.g., Stacy and Koenig 1990), and they occur in taxa as diverse as ants (Order Hymenoptera; Reeve and Ratnieks 1993) and hawks (e.g., *Buteo galapagoensis*; Faaborg and Bednarz 1990). Cooperative breeding among birds can include multiple parents that lay eggs in a single nest (*Crotophaga sulcirostris*; Vehrencamp 1978), large breeding collectives that include multiple breeding pairs and numerous non-breeding individuals (*Melanerpes formicivorous*; Koenig et al. 1995), or colony-nesting species with helpers assisting related clans (*Merops bullockoides*; Emlen and Wrege 1989). Cooperation appears to be most commonly exhibited as groups comprised of parents and offspring that work together to rear related young (e.g., *Picoides borealis*; Walters 1990). This behavior is rare, as ~2.5% of birds are considered to be cooperative breeders (Brown 1987).

Several life history characteristics are commonly associated with cooperative breeding (Du Plessis et al. 1995). Some cooperatively breeding birds are year-round territorial species with young that have extended parental dependence (Brown 1987, Stacey and Koenig 1990). Cooperation can also occur in situations with limitations in breeding resources or territories, in which potential dispersers are considered to be ecologically constrained from breeding independently (Selander 1971, Brown 1974, Gaston 1978, Stacey 1979, Emlen 1982). This concept was first presented as *habitat saturation* (Brown 1974) and later articulated as the *ecological constraints hypothesis* (Emlen 1982). A conceptual model of the hypothesis was described as a situation in which all available habitats already host territories that are maximally compressed in size (Brown 1987). Alternatively, some suggested that cooperation must have originated on the natal territory, and that potential dispersers delayed dispersing because the *benefits of philopatry* outweighed those of immediate dispersal (Stacey and Ligon 1987, 1991).

We present the first observations of cooperative breeding by the Society Kingfisher (*Todiramphus veneratus*). The Society Kingfisher is a member of a genus that includes 11 imperiled species (near threatened or above, IUCN 2008) of the 21 recognized (Clements 2007). We present three lines of evidence for cooperation in the Society Kingfisher. First, we describe direct observations of helping behaviors at nests. Second, we report observations of cooperative groups of birds throughout the study area and during the breeding season. Finally, we provide population density estimates and compare those to densities reported for other Pacific *Todiramphus* species to illustrate the potential for habitat saturation.

METHODS

We observed Society Kingfishers on the island of Moorea (17° 32′ S, 149° 50′ W) during surveys

[1] Department of Fisheries and Wildlife Sciences, 302 Anheuser-Busch Natural Resources Building, University of Missouri, Columbia, MO 65211, USA.

[2] Société d'Ornithologie de Polynésie ''Manu'', B.P. 8699, 98719 Taravao, Tahiti, Polynésie Française.

[3] Corresponding author; e-mail: keslerd@missouri.edu

FIG. 1. Copulation with three Society Kingfishers present on 31 December 2008 on the island of Moorea, French Polynesia. (Photograph by T. Ghestemme.)

and visits in November and December 2008, and January 2009. We described cooperative behaviors observed on two territories during nest excavation, incubation, and brood rearing phases (17° 32′ 11″ S, 149° 49′ 46″ W; and 17° 32′ 26″ S, 149° 47′ 20′ W). Each observation period lasted ~30 min, and dates and times associated with each behavior are reported.

We conducted variable distance point-transect surveys (Buckland et al. 1993) of Moorea's landbirds at 46 stations in undeveloped upland forests. Stations were separated by 200 m. The distance was estimated to all landbirds detected by visual or auditory means during a 10-min observation period at each station. We also recorded the number of kingfishers present when detected outside of prescribed observation periods. Point-transect data were analyzed with Program DISTANCE (Thomas et al. 2006) to estimate the density of Society Kingfishers on the island of Moorea. We pooled observations into 25-m groups and conducted the analysis with a half-normal key, truncation at 100 m, and default model selection adjustment routine (Akaike's Information Criteria; AIC_c; Burnham and Anderson 2002). Limited detections reduced potential adjustment parameters to two, but the results were intuitively appealing and Chi-square goodness of fit tests indicated the approach was reasonable ($\chi^2 = 3.66$, df = 2, $P = 0.16$).

RESULTS

On 25 (1510–1612 hrs), 26 (1045–1125 hrs), and 27 (0720–0815 hrs) November 2008 we observed three Society Kingfishers cooperatively excavating nest cavities in the central and southeastern regions of Moorea. Three kingfishers were perched in close proximity (<2 m) on each occasion. All group members flew to the trees (*Neonauclea fosteri*) of interest and struck the main stem with their beaks. Nest excavation was accompanied by loud calling, and quieter growling and warbling vocalizations typical of Pacific kingfishers. Two individuals consistently perched closer together (within 50 cm) and struck the cavity more often than the third bird, which only struck the tree once during each observation period. Two birds were observed excavating a cavity without a third individual present on two other territories. On 31 December (0925 hrs), two birds copulated (Fig. 1) while the third bird passively perched within 10 cm. No aggressive behaviors were observed during nest excavations or copulations. Two of three group members were

marked with individual-specific combinations of colored plastic leg bands on 13 January 2009 on the central region territory. On 13 (1040–1125 hrs), 14 (1500–1630 hrs), and 15 (1600–1715 hrs) January, at least three birds (2 color banded and 1 unbanded) were observed entering the nest cavity and incubating. The same 2 color-banded and 1 unbanded group members were also observed delivering food items to the nest on 19 February (0630–0830 hrs).

Observations of three-bird groups of Society Kingfishers throughout the island of Moorea provided further support for cooperation. Kingfishers were detected at 61% of the point-transect stations during island-wide surveys. Of the birds visually observed, we encountered seven three-bird groups and seven two-bird groups. Three-bird groups were observed on an additional four territories outside of survey periods. The distance-based analyses indicated densities of 2.4 kingfishers/ha (95% CI = 1.6–3.5). These results suggest Society Kingfisher territories on Moorea were 0.82 ha (95% CI = 0.57–1.19) in size for pairs or 1.23 ha (95% CI = 0.85–1.90) for trios, based on multiplying density estimates by group size. No groups were observed with more than three individuals.

DISCUSSION

Our observations of cooperative nest excavations and food delivery by Society Kingfishers are congruent with cooperative behaviors reported for other birds, and we suggest the species qualifies as a cooperative breeder. Cooperative breeding has been described in other *Todiramphus* kingfishers of Pacific Oceania. Beckon (1987) reported three-bird nest excavation by Collared Kingfishers (*T. chloris*), and substantial work was directed at cooperative behaviors of Micronesian Kingfishers (*T. cinnamominus*) (Kesler and Haig 2005, 2007a). This behavior is relatively common among other Coraciiformes. Cooperative breeding has been documented for Rufous Hornbills (*Buceros hydrocorax*) (Witmer 1993), White-fronted Bee-eaters (*Merops bullockoides*) (Emlen and Wrege 1989), Laughing Kookaburras (*Dacelo novaeguineae*) (Legge and Cockburn 2000), and Pied Kingfishers (*Ceryle rudis*) (Reyer 1980) among others.

Our distance-based results indicated a Society Kingfisher population density that was higher than for other Pacific kingfisher species in similarly structured habitats. Mean territory size was 5.9 ha for cooperatively breeding Micronesian Kingfishers (Kesler and Haig 2007b, c) and 6–10 ha for Tuamotu Kingfishers (*Todiramphus gambieri*; Coulombe and Kesler, in prep). Kingfishers exclude neighboring conspecifics from their territories, and territory sizes translate to population densities of 0.5 Micronesian Kingfishers/ha (assuming territories with 3 birds), and 0.2 Tuamotu Kingfishers/ha (assuming a breeding pair). Our results indicate population densities of Society Kingfishers on Moorea that are 4.4 times higher than cooperatively breeding Micronesian Kingfishers and 6.7 times higher than breeding pairs of Tuamotu Kingfishers. This high density of Society Kingfishers on Moorea may overwhelm breeding resources, saturate habitats with territories, and lead to the ecological constraints previously suggested to cause cooperation in other species (Emlen 1982, Walters et al. 1992).

Cooperative breeders provide opportunities to simultaneously test fundamental theories in behavioral ecology and conservation biology because both management and cooperative breeding theory often focus on limited resources (Walters et al. 1992, Komdeur 1994). For example, much has been learned about conservation and evolution of cooperative sociality in the endangered Red-cockaded Woodpecker (*Picoides borealis*) (Connor et al. 2001). Conservation managers in French Polynesia should consider the importance of identifying and managing limited kingfisher resources to maintain robust populations. Cooperative breeding also has the potential to influence population resilience by creating a reserve set of adult helpers that are poised to breed when opportunities are presented, which can buffer the effects of environmental or demographic stochasticity (Walters et al. 2002, Kesler and Haig 2007a).

Society Kingfishers were abundant in the undisturbed upland forests of Moorea and Tahiti (Gouni and Zysman 2007), and it is somewhat striking that cooperative behaviors were not previously described. A similar lack of knowledge persists for many Pacific birds despite the immense contributions that island species have made to biological understanding. We advocate for added focus on the basic natural history of birds in remote and threatened regions, including the islands of Pacific Oceania.

ACKNOWLEDGMENTS

We are indebted to all who provided financial, material, and technical support to the project, including members of

Société d'Ornithologie de Polynésie ''Manu'', the government of French Polynesia, and ESRI Conservation Grants Program. We extend special thanks to Stephan Vanderstokt, Jeannine Gouni, Jean-Marie Gouni, and Christophe Noiret for their important logistical contributions. Additionally, we thank Jeff Walters, Allison Cox, and the anonymous reviewers who helped improve the quality of the manuscript.

LITERATURE CITED

BECKON, W. N. 1987. Evidence of cooperative nest excavation by the White-collared Kingfisher in Fiji. Ibis 129:391–392.

BROWN, J. L. 1974. Alternate routes to sociality in jays–with a theory for the evolution of altruism and communal breeding. American Zoologist 14:63–80.

BROWN, J. L. 1987. Helping and communal breeding in birds: ecology and evolution. Princeton University Press, Princeton, New Jersey, USA.

BUCKLAND, S., D. ANDERSON, K. BURNHAM, AND J. LAAKE. 1993. Empirical models for the spatial distribution of wildlife. Journal of Applied Ecology 30:478–495.

BURNHAM, K. P. AND D. R. ANDERSON. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Springer-Verlag, New York, USA.

CLEMENTS, J. F. 2007. The Clements checklist of birds of the world. Sixth Edition. Comstock Publishing Associates, Ithaca, New York, USA.

COCKBURN, A. 2004. Mating systems and sexual conflict. Pages 81–101 *in* Ecology and evolution of cooperative breeding in birds (W. D. Koenig and J. L. Dickinson, Editors). Cambridge University Press, New York, USA.

COCKBURN, A. 2006. Prevalence of different models of parental care in birds. Proceedings of the Royal Society of London, Series B 273:1375–1383.

CONNER, R. N., D. C. RUDOLPH, AND J. R. WALTERS. 2001. The Red-cockaded Woodpecker: surviving in a fire-maintained ecosystem. University of Texas Press, Austin, USA.

COULOMBE, G. AND D. C. KESLER. In prep. Multiscale resource selection in critically endangered Tuamotu Kingfishers. Biological Conservation: In press.

DU PLESSIS, M. A., W. R. SIEGFRIED, AND A. J. ARMSTRONG. 1995. Ecological and life-history correlates of cooperative breeding in South African birds. Oecologia 102:180–188.

EMLEN, S. T. 1982. The evolution of helping. I. An ecological constraints model. American Naturalist 119:29–39.

EMLEN, S. T. AND P. WREGE. 1989. A test of alternate hypotheses for helping behavior in White-fronted Bee-eaters of Kenya. Behavioral Ecology and Sociobiology 25:303–319.

FAABORG, J. AND J. C. BEDNARZ. 1990. Galapagos and Harris' hawks: divergent causes of sociality in two raptors. Pages 357–384 *in* Cooperative breeding in birds: long-term studies of ecology and behavior (P. B. Stacey and W. D. Koenig, Editors). Cambridge University Press, Cambridge, United Kingdom.

GASTON, A. J. 1978. The evolution of group territorial behavior and cooperative breeding. American Naturalist 112:1091–1100.

GOUNI, A. AND T. ZYSMAN. 2007. Oiseaux du Fenua, Tahiti et ses îles. Théthys Editions, Paris, France.

INTERNATIONAL UNION FOR THE CONSERVATION OF NATURE (IUCN). 2008. Red list of threatened species. International Union for Conservation and Natural Resources, Gland, Switzerland. www.iucnredlist.org (accessed 1 January 2009).

KESLER, D. C. AND S. M. HAIG. 2005. Selection of arboreal termitaria for nesting by cooperatively breeding Pohnpei Micronesian Kingfishers. Ibis 147:188–196.

KESLER, D. C. AND S. M. HAIG. 2007a. Conservation biology for suites of species: population demography for the *Todiramphus* kingfishers. Biological Conservation 136:520–530.

KESLER, D. C. AND S. M. HAIG. 2007b. Multi-scale resource use and selection in cooperatively breeding Micronesian Kingfishers. Journal of Wildlife Management 71:765–772.

KESLER, D. C. AND S. M. HAIG. 2007c. Territoriality, prospecting, and dispersal in cooperatively breeding Micronesian Kingfishers (*Todiramphus cinnamominus reichenbachii*). Auk 124:381–395.

KOENIG, W. D. AND J. L. DICKINSON. 2004. Ecology and evolution of cooperative breeding in birds. Cambridge University Press, New York, USA.

KOENIG, W. D., P. B. STACEY, M. T. STANBACK, AND R. L. MUMME. 1995. Acorn Woodpecker (*Melanerpes formicivorus*). The birds of North America. Number 194.

KOMDEUR, J. 1994. Experimental evidence for helping and hindering by previous offspring in the cooperative-breeding Seychelles Warbler (*Acrocephalus sechellensis*). Behavioral Ecology and Sociobiology 34:175–186.

LEGGE, S. AND A. COCKBURN. 2000. Social and mating system of cooperatively breeding Laughing Kookaburras (*Dacelo novaeguineae*). Behavioral Ecology and Sociobiology 47:220–229.

REEVE, H. K. AND F. L. W. RATNIEKS. 1993. Queen-queen conflict in polygynous societies: mutual tolerance and reproductive skew. Pages 45–85 *in* Queen number and sociality in insects (L. Keller, Editor). Oxford University Press, Oxford, United Kingdom.

REYER, H. 1980. Flexible helper structure as an ecological adaptation in the Pied Kingfisher (*Ceryle rudis*). Behavioral Ecology and Sociobiology 6:219–227.

SELANDER, R. K. 1971. Systematics and speciation in birds. Pages 57–147 *in* Avian biology (D. S. Farner and J. R. King, Editors). Volume 1. Academic Press, New York, USA.

SKUTCH, A. F. 1935. Helpers at the nest. Auk 52:257–273.

STACEY, P. B. 1979. Habitat saturation and communal breeding in the Acorn Woodpecker. Animal Behaviour 27:1153–1166.

STACEY, P. B. AND W. D. KOENIG. 1990. Cooperative breeding in birds: long-term studies of ecology and

behavior. Cambridge University Press, New York, USA.

STACEY, P. B. AND J. D. LIGON. 1987. Territory quality and dispersal options in the Acorn Woodpecker, and a challenge to the habitat-saturation model of cooperative breeding. American Naturalist 130:654–676.

STACEY, P. B. AND J. D. LIGON. 1991. The benefits-of-philopatry hypothesis for the evolution of cooperative breeding: variation in territory quality and group size effects. American Naturalist 137: 831–846.

THOMAS, L., J. L. LAAKE, S. STRINDBERG, F. F. C. MARQUES, S. T. BUCKLAND, D. L. BORCHERS, D. R. ANDERSON, K. P. BURNHAM, S. L. HEDLEY, J. H. POLLARD, J. R. B. BISHOP, AND T. A. MARQUES. 2006. DISTANCE 5, Release 2. Research Unit for Wildlife Population Assessment, University of St. Andrews, United Kingdom.

VEHRENCAMP, S. 1978. The adaptive significance of communal nesting in Groove-billed Anis (*Crotophaga crotophaga sulcirostris*). Behavioral Ecology and Sociobiology 4:1–33.

WALTERS, J. R. 1990. Red-cockaded Woodpeckers: a 'primitive' cooperative breeder. Pages 67–102 *in* Cooperative breeding in birds: long-term studies of ecology and behavior (P. B. Stacey and W. D. Koenig, Editors). Cambridge University Press, New York, USA.

WALTERS, J. R., C. K. COPEYON, AND J. H. CARTER III. 1992. Test of the ecological basis of cooperative breeding in Red-cockaded Woodpeckers. Auk 109:90–97.

WALTERS, J. R., L. CROWDER, AND J. PRIDDY. 2002. Population viability analysis for Red-cockaded Woodpeckers using an individual-based model. Ecological Applications 12:249–260.

WITMER, M. C. 1993. Cooperative breeding by Rufous Hornbills on Mindanao Island, Philippines. Auk 110:933–936.