California. Dissertation. University of California, Berkeley.

PITELKA, F. A. 1942. Territoriality and related problems in North American hummingbirds. Condor 44:189–204.

POWERS, D. R. 1987. Effects of variation in food quality on the breeding territoriality of the male Anna's Hummingbird. Condor 89:103–111.

RYSER, F. A. 1985. Birds of the Great Basin: a natural history. University of Nevada Press, Reno, USA.

SALLABANKS, R., J. B. HAUFLER, AND C. A. MEHL. 2006. Influence of forest vegetation structure on avian community composition in west-central Idaho. Wildlife Society Bulletin 34:1079–1093.

STILES, F. G., D. L. ALTSHULER, AND R. DUDLEY. 2005. Wing morphology and flight behavior of some North American hummingbird species. Auk 122:872–886.

TAMM, S. 1985. Breeding territory quality and agonistic behavior: effects of energy availability and intruder pressure in hummingbirds. Behavioral Ecology and Sociobiology 16:203–207.

TAMM, S., D. P. ARMSTRONG, AND Z. J. TOOZE. 1989. Display behavior of male Calliope Hummingbirds during the breeding season. Condor 91:272–279.

The Wilson Journal of Ornithology 126(1):128–133, 2014

Feeding Rates, Double Brooding, Nest Reuse, and Seasonal Fecundity of Eastern Wood-Pewees in the Missouri Ozarks

Sarah W. Kendrick,[1,3] Frank R. Thompson III,[2] and Jennifer L. Reidy[1]

ABSTRACT.—Despite being widespread and abundant, little is known about the breeding ecology and natural history of the Eastern Wood-Pewee (*Contopus virens*), in part because nests are often high in the canopy, difficult to view, and adults are monomorphic. We monitored nests of Eastern Wood-Pewees and recorded the feeding rate of nestlings by adults as part of a larger study on breeding demography of Eastern Wood-Pewees across a gradient of savanna, woodland, and forest in the Missouri Ozarks in 2010–2011. We monitored 287 nests between 26 May and 22 August and conducted feeding rate observations for 54 nests with nestlings. There was an 88-day nesting season with peaks of nest activity on 24 June and 22 July. We recorded 19 cases of double brooding and nine cases of within-season nest reuse. Seasonal fecundity was 2.2 fledglings per territory. The frequency of parental feeding visits increased with nestling age. These are additional observations of nest reuse, nesting cycle lengths, and breeding season length for Eastern Wood-Pewees; future demographical research of marked individuals will continue to fill in gaps in breeding ecology for this common and widespread flycatcher.

Received 12 July 2013. Accepted 5 November 2013.

Key words: breeding ecology, double brooding, Eastern Wood-Pewee, feeding rate, Missouri Ozarks, nest reuse, seasonal fecundity.

Eastern Wood-Pewees (*Contopus virens*; hereafter ''pewee'') are vocal and abundant Neotropical migrant songbirds that breed in a variety of wooded habitats across the eastern United States north into the southern regions of Canada (McCarty 1996). Because pewees are abundant across a range of habitats, we can observe them to evaluate effects of forest disturbance and management on demographics such as productivity. Several studies evaluating abundance and nest survival in relation to forest management have included pewees (Davis et al. 2000; Knutson et al. 2004; Brawn 2006; Grundel and Pavlovic 2007a,b; Newell and Rodewald 2011, 2012), but, with the exception of Newell et al. (2013), studies have not focused on pewee breeding ecology. Thus, there are large gaps in our knowledge of their natural history possibly because of an inability to easily reach high nests, which average 18 m in the Missouri Ozarks (range: 2.6–26.6 m, $n = 310$; Kendrick et al. 2013). Our objective was to acquire additional knowledge of the demographics of Eastern Wood-Pewees including nesting dates, number of nest attempts, breeding season length, and parental feeding rates, because these demographic data are lacking in the literature. Feeding rate data are important common measures of parental behavior (Taylor and Kershner 1991, Darveau et al. 1993, Whitehead and Taylor 2002, Altman and Sallabanks 2012), and the frequency of parental nest

---

[1] Department of Fisheries and Wildlife, University of Missouri, 302 ABNR Building, Columbia, MO 65211, USA.

[2] U.S. Department of Agriculture Forest Service, Northern Research Station, 202 ABNR Building, University of Missouri, Columbia, MO 65211, USA.

[3] Corresponding author; e-mail: sarahwkendrick@gmail.com

visits may affect nest predation (Martin et al. 2000). Nesting dates, number of nest attempts, and occurrence of double brooding are important parameters for estimating species productivity and population viability (Donovan and Thompson 2001, Etterson et al. 2011). Here we report our observations of nesting dates of pewees, nest attempts and double brooding, nest reuse, and parental feeding rates collected as part of a larger study on pewee demography in savanna, woodland, and forest in Missouri (Kendrick et al. 2013).

METHODS

Study Area.—We studied pewees in the Ozark Highlands of Missouri. The region is equally divided between steep and rolling hills, and gently rolling plains (McNab and Avers 1994). The region includes oak (*Quercus* spp.)-hickory (*Carya* spp.) and oak-hickory-pine (*Pinus echinata*) forest, bluestem (*Andropogon gerardii*, *Schizachyrium scoparium*) prairie, and eastern redcedar (*Juniperus virginiana*) glades (McNab and Avers 1994). We selected 13 sites across the region on lands owned by the Missouri Department of Conservation, the Missouri Department of Natural Resources, The Nature Conservancy, and the U.S. Department of Agriculture Forest Service. More information on site selection and the characteristics of savanna, woodland, and forest sites can be found in Kendrick et al. (2013).

We began this research as part of a study investigating the response of breeding birds to savanna and woodland management in 2009, but intensified and focused our efforts on pewees in 2010 and 2011 (Kendrick et al. 2013). We searched for pewee nests between early May and mid-August using parental behavior within a territory. Nests were monitored every 3–4 days, or daily near predicted fledge date, to determine if nests were active, the stage of the nest, and nest contents. We constructed a telescoping video pole that included a Spiderbeam antenna pole (WiMo; Herxheim, Germany) and a wireless camera and monitor (Defender Phoenix surveillance system; Defender, Niagara Falls, Ontario) to view nest contents up to 16.5 m high. A team of two people used the pole to determine nest contents once per nest stage (i.e., incubation and nestling stages). Lay and hatch dates were estimated based on observations from video pole checks, parental behavior, and nestling size. We did not use the video pole if we detected Blue Jays (*Cyanocitta cristata*), American Crows (*Corvus brachyrhynchos*), or Brown-headed Cowbirds (*Molothrus ater*) to minimize time at the nest and attention drawn to the nest. We considered a nest to be successful if we verified at least one host fledgling. We attempted to locate a re-nesting attempt for a pair in a territory when a nest failed. In 2010, we focused on observing parental behavior of pewees to locate and monitor nests, distinguish territories, and monitor pairs throughout the breeding season; in 2011, we intensified our effort by monitoring territories with successful nests to determine if pairs attempted second broods. We did not uniquely color-band birds, but by closely monitoring territories and the timing of nest fates, and witnessing removal of nest material from failed nests to build second nests, we believe we accurately detected re-nesting and double brooding attempts.

We used the modified productivity model of Farnsworth and Simons (2001, 2005) to estimate seasonal fecundity. Model assumptions are: (1) clutch size is constant for all nests, (2) a female nests as many times as possible if time remains in the breeding season, (3) daily nest survival is constant throughout the breeding season and between stages, (4) all eggs hatch and all young fledge in successful nests, (5) no adult mortality occurs in the breeding season, and (6) the time it takes an adult to initiate a re-nest attempt does not vary (Farnsworth and Simons 2001). We only used data from nests in 2010 and 2011 for the nesting parameters reported here because of increased effort in these years to monitor number of attempts and nest contents; however, the daily nest survival value for the productivity model was taken from Kendrick et al. (2013) and is based on all monitored nests 2009–2011 (n = 310).

We measured feeding rate by observing nests across a range of nestling ages for 1 hr between sunrise and 1200 CST in 2010 and 2011. We recorded the arrival time and duration of every visit made by either adult, and we recorded number of nestlings in the nest. We also observed behavior at the nest (e.g., if the parent brooded nestlings after feeding). We fit a general linear model to determine the effects of nestling age and number of nestlings on the number of feeding visits/hr; because only three of 39 observations of feeding rate were repeat observations on the same nest, we did not account for repeated visits in the model with an additional covariance term.

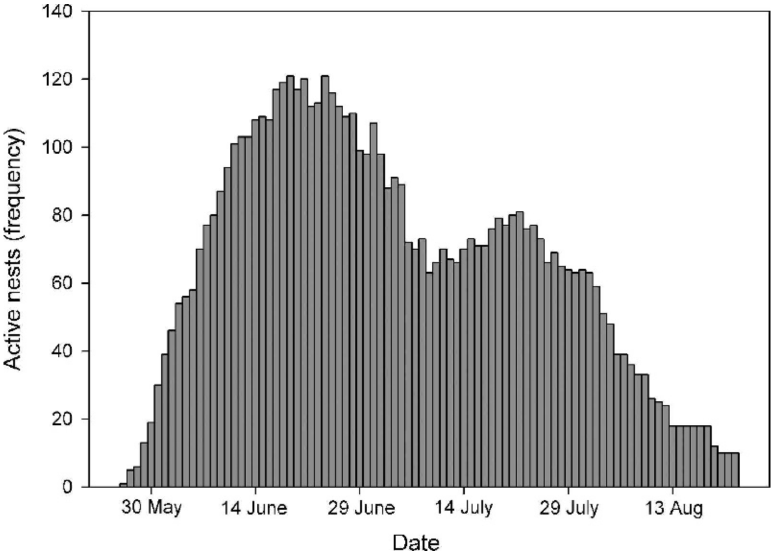

FIG. 1. Frequency of active nests of Eastern Wood-Pewees by date for nests found in the Missouri Ozarks, 2010–2011.

RESULTS

We monitored 69 and 217 nests in 2010 and 2011, respectively. The earliest active nest we observed (probably in laying stage) was 26 May and latest active nest was 22 August (Fig. 1), similar to breeding season dates for pewees in Ohio (Newell et al. 2013). The greatest number of active nests for 2010 and 2011 pooled was on June 24 with a secondary peak on July 22; the breeding season lasted 88 days (Fig. 1). Based on 70 successful nests found in the building stage, we estimated the mean length of the nesting cycle from the beginning of a clutch to fledging was 33.5 days (SE = 0.31), including 14.1 days (SE = 0.42) for the incubation stage and 15.4 days (SE = 0.46) for the nestling stage.

We observed multiple nesting attempts after failure; 53 pairs attempted a second nest and five attempted a third nest. We documented an average of 8.15 days (SE = 0.6; $n = 34$) between nest failure and the first egg of a re-nesting attempt. We never observed pewees reusing a nest after a failure. Of 92 territories that successfully fledged young in 2011, 19 (21%) attempted a second brood but only three were successful. We documented an average of 9.4 days (SE = 0.92; $n = 14$) between a successful nest and the first egg of a re-nesting attempt. One of the 19 pairs made three unsuccessful attempts for a second brood, thus four nest attempts was the maximum we observed for any territory. Nine pairs reused their first successful nest for a second brood attempt, but none of these were successful.

We observed both adults tending to fledglings in the immediate nest area even after the second nest was active. We observed adults adding material to nests that had previously fledged young before laying another clutch. Not all second broods were initiated early in the season; the latest double brood attempt was found early in the incubation stage on 1 August. Because we monitored nests at different sites every year, we were unable to examine whether pewees reused nests in subsequent years. For pairs that did not reuse nests, mean distance between the first successful nest and second nest was 42.7 m (range: 23.54–72.56 m; $n = 9$).

We estimated seasonal fecundity to be 2.2 fledglings per female based on the Farnsworth and Simons model (2001, 2005). The seasonal fecundity estimate was based on a daily nest survival of 0.98 (95% CI: 0.97–0.98, $n = 310$; Kendrick et al. 2013), an average clutch size of 2.6 ($n = 110$; Kendrick et al. 2013), a maximum of four nesting attempts per female per breeding season, a maximum of two broods per female per breeding season, a 100% probability of re-nesting after nest failure if enough time remained in the breeding season, and an average of 2.2 fledglings per successful nest ($n = 64$; Kendrick et al. 2013) in

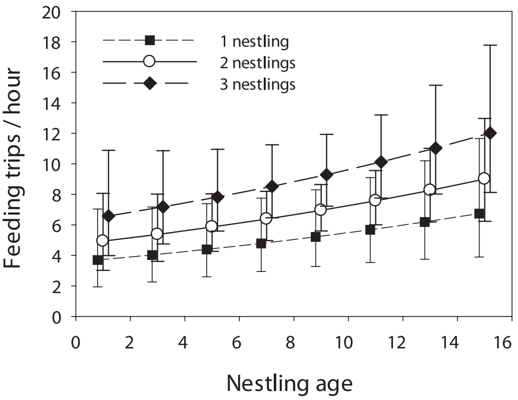

FIG. 2. Effect of nestling age on the frequency of adult feeding visits to the nest by Eastern Wood-Pewees in the Missouri Ozarks, 2010–2011.

addition to the nesting parameters reported above to estimate seasonal fecundity.

We recorded parental feeding visits for 54 nests with nestlings ranging in age from 1–15 days. Mean feeding rate was 8.03 visits/hr (SE = 0.61) and mean duration of nest visits was 1.32 min (SE = 0.22). We modeled effects of nestling age and number of nestlings on a subset of 39 nest observations for which we knew the number of nestlings. A negative binomial distribution was more suitable than a Poisson or normal distribution; there was no evidence of lack of fit of the model based on the overdispersion parameter ($\hat{c}$ = 1.07). The number of nestlings and nestling age had marginally significant effects ($P = 0.062$, $P = 0.11$; respectively) and feeding visits increased with more nestlings and older nestlings (Fig. 2). We could not determine feeding rates by sex, because we did not color-band adults, but we did confirm both adults feeding at the nest individually (observed when parents switched places at the nest to feed) and simultaneously. We observed adults sitting on nestlings that were up to 8 days old after feeding.

DISCUSSION

We located and monitored a large sample of nests and determined pewees made up to four nest attempts; we documented additional instances of double brooding and multiple cases of within-season nest reuse (Newell et al. 2013), and calculated the first known estimate of seasonal fecundity for the Eastern Wood-Pewee in the Missouri Ozarks. Basic demographic data such as breeding season and nesting cycle lengths from a large sample have not been previously reported for the pewee. Old accounts from a handful of nests report an incubation period of 12–13 days and a nestling stage of 15–18 days (Bent 1942), both period lengths within about 1 day of our findings. The pewee nesting cycle of 33.5 days includes a laying stage of ~4 days. We previously documented a mean clutch size of 2.6 (range: 1–3; $n = 111$; Kendrick et al. 2013). Some flycatchers have been found to lay one egg per day (Oppenheimer et al. 1996); thus, our estimate of a laying stage length of ~4 days may be a slight overestimation.

The number of attempts we reported is determined from the minimum number of nest attempts made, because we are not confident we found every attempt made for each pair. For example, a nest found later in the breeding season in a territory without any previous documented attempts is difficult to report as a second or third attempt when we may not have found previous nest attempts. Acadian Flycatchers (*Empidonax virescens*) will sometimes make up to five re-nesting attempts after a failure (Whitehead and Taylor 2002). Nest reuse in subsequent years has been reported for pewees (Bent 1942), and nest reuse between years also occurs in Western Wood-Pewees (*Contopus sordidulus*; Bent 1942, Curson et al. 1996). Benefits of within-season nest reuse may include less time and energy that pewees must spend searching for new nest locations and materials (Curson et al. 1996), whereas drawbacks include increased nest predation (Lima and Dill 1990) and potential nest failure because of structural damage (Bergin 1997). Structural damage may be less of a concern for within-season nest reuse than reuse in subsequent years. While individuals were not color-banded, we believe that we observed double brooding based on nest reuse, observed territory boundaries, known nesting status of neighboring territories, removal of material from previous nest attempts for the construction of another nest, and parental care of fledglings that remained in the territory while a second nest was initiated.

Basic information on clutch size, number of young fledged, and re-nesting attempts allowed us to calculate an estimate of seasonal fecundity, which is a key component of population models. Our estimate of 2.24 is similar to the 2.03 and 2.23 fledglings per female for monogamous and polygynous pewees, respectively, in Ohio (Newell et al. 2013). Our estimated fecundity was also similar to a seasonal fecundity of 2.5 for Acadian Flycatchers (Fauth and Cabe 2005) and previous-season fecundity of 2.27 for territory-faithful female Willow Flycatchers (*Empidonax traillii*; Sedgwick 2004). As expected, feeding rates increased with nestling age. Increased activity at the nest during the nestling stage may explain higher predation rates observed during the nestling stage (Kendrick et al. 2013). Feeding rates in Ohio (Newell et al. 2013) were almost twice those we observed, but mean brood size was similar, so it is unclear what is driving this difference or what the consequences are. Different provisioning rates could reflect subtle differences in methodologies between studies or different prey quality or availability and could result in differences in nestling condition or size; however, we did not measure nestlings.

We report demographic information about Eastern Wood-Pewees to contribute to our understanding of the species and Neotropical migratory birds in general. We provided information on the occurrence of double brooding and seasonal fecundity of pewees; knowledge of both of these aspects of breeding biology is limited for Neotropical migrants (Faaborg et al. 2010). We think future research to address remaining gaps in breeding biology should include marking adults to enable identification of individuals and a better understanding of parental roles and singing behavior of males and females as well as other aspects of demographics such as survival.

ACKNOWLEDGMENTS

Funding for this research was provided by the U.S. Department of Agriculture Forest Service Northern Research Station. We thank the Missouri Department of Conservation, the Missouri Department of Natural Resources, The Nature Conservancy, and Mark Twain National Forest for project support.

LITERATURE CITED

ALTMAN, B. AND R. SALLABANKS. 2012. Olive-sided Flycatcher (*Contopus cooperi*). The birds of North America. Number 502.

BENT, A. C. 1942. Life histories of North American flycatchers, larks, swallows, and their allies. General Publishing Company, Toronto, Ontario, Canada.

BERGIN, T. M. 1997. Nest reuse by Western Kingbirds. Wilson Bulletin 109:735–737.

BRAWN, J. D. 2006. Effects of restoring oak savannas on bird communities and populations. Conservation Biology 20:460–469.

CURSON, D. R., C. B. GOGUEN, AND N. E. MATHEWS. 1996. Nest-site reuse in the Western Wood-Pewee. Wilson Bulletin 108:378–380.

DAVIS, M. A., D. W. PETERSON, P. B. REICH, M. CROZIER, T. QUERY, E. MITCHELL, J. HUNTINGTON, AND P. BAZAKAS. 2000. Restoring savanna using fire: impact on the breeding bird community. Restoration Ecology 8:30–40.

DARVEAU, M., G. GAUTHIER, J. L. DESGRANGES, AND Y. MAUFFETTE. 1993. Nesting success, nest sites, and parental care of the Least Flycatcher in declining maple forests. Canadian Journal of Zoology 71:1592–1601.

DONOVAN, T. M. AND F. R. THOMPSON III. 2001. Modeling the ecological trap hypothesis: a habitat and demographic analysis for migrant songbirds. Ecological Applications 11:871–882.

ETTERSON, M. A., S. N. ELLIS-FELEGE, D. EVERS, G. GAUTHIER, J. A. GRZYBOWSKI, B. J. MATTSSON, L. R. NAGY, B. J. OLSEN, C. M. PEASE, M. P. VAN DER BURG, AND A. POTVIEN. 2011. Modeling fecundity in birds: conceptual overview, current models, and considerations for future developments, Ecological Modeling 222:2178–2190.

FAABORG, J, R. HOLMES, A. ANDERS, K. BILDSTEIN, K. DUGGER, S. GAUTHREAUX, P. HEGLUND, K. HOBSON, A. JAHN, D. JOHNSON, S. LATTA, D. LEVEY, P. MARRA, E. NOL, S. ROTHSTEIN, T. SHERRY, T. S. SILLETT, F. THOMPSON III, N. WARNOCK. 2010. Conserving migratory landbirds in the New World: do we know enough? Ecological Applications 20:398–418.

FARNSWORTH, G. L. AND T. R. SIMONS. 2001. How many baskets? Clutch sizes that maximize annual fecundity of multiple-brooded birds. Auk 118:973–982.

FARNSWORTH, G. L. AND T. R. SIMONS. 2005. Relationship between Mayfield nest-survival estimates and seasonal fecundity: a cautionary reply. Auk 122:1000–1001.

FAUTH, P. T. AND P. R. CABE. 2005. Reproductive success of Acadian Flycatchers in the Blue Ridge Mountains of Virginia. Journal of Field Ornithology 76:150–157.

GRUNDEL, R. AND N. B. PAVLOVIC. 2007a. Response of bird species densities to habitat structure and fire history along a Midwestern open-forest gradient. Condor 109:734–749.

GRUNDEL, R. AND N. B. PAVLOVIC. 2007b. Distinctiveness, use, and value of midwestern oak savannas and woodlands as avian habitats. Auk 124:969–985.

KENDRICK, S.W., F. R. THOMPSON III, AND J. L. REIDY. 2013. Eastern Wood-Pewee (*Contopus virens*) breeding demography across a gradient of savanna, woodland, and forest in the Missouri Ozarks. Auk 130:355–363.

KNUTSON, M. G., G. J. NIEMI, W. E. NEWTON, AND M. A. FRIBERG. 2004. Avian nest success in Midwestern forests fragmented by agriculture. Condor 106:116–130.

LIMA, S. L. AND L. M. DILL. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. Canadian Journal of Zoology 68:619–640.

MARTIN, T. E., J. SCOTT, AND C. MENGE. 2000. Nest predation increases with parental activity: separating nest site and parental activity effects. Proceedings of the Royal Society of London, Series B: Biological Sciences 267:2287.

MCCARTY, J. P. 1996. Eastern Wood-Pewee (*Contopus virens*). The birds of North America. Number 245.

McNab, W. H. and P. E. Avers. 1994. Ecological subregions of the United States, section descriptions. USDA, Administrative Publication WO-WSA-5, Washington D.C., USA.

Newell, F. L. and A. D. Rodewald. 2011. Role of topography, canopy structure, and floristics in nest-site selection and nesting success of canopy songbirds. Forest Ecology and Management 262:739–749.

Newell, F. L. and A. D. Rodewald. 2012. Management for oak regeneration: short-term effects on the bird community and suitability of shelterwood harvests for canopy songbirds. Journal of Wildlife Management 76:683–69311.

Newell, F. L., A. N. K. Haiman, D. L. Narango, J. Means Elder, L. D. Leonhard, J. Philhower-Gillen, A. M. Johnson, and A. D. Rodewald. 2013. Occurrence of polygyny and double brooding in the Eastern Wood-Pewee. Wilson Journal of Ornithology 125:251–259.

Oppenheimer, S. D., M. E. Pereyra, and M. L. Morton. Egg laying in Dusky Flycatchers and White-crowned Sparrows. 1996. Condor 98:428–430.

Sedgwick, J. A. 2004. Site fidelity, territory fidelity, and natal philopatry in Willow Flycatchers (*Empidonax traillii*). Auk 121:1103–1121.

Taylor, W. K. and M. A. Kershner. 1991. Breeding biology of the Great Crested Flycatcher in central Florida. Journal of Field Ornithology: 62:28.

Whitehead, D. R. and T. Taylor. 2002. Acadian Flycatcher (*Empidonax virescens*). The birds of North America. Number 614.

The Wilson Journal of Ornithology 126(1):133–139, 2014

New Caledonian Crows' (*Corvus moneduloides*) Pandanus Tool Designs: Diversification or Independent Invention?

Gavin R. Hunt[1]

ABSTRACT.—New Caledonian Crows (*Corvus moneduloides*) manufacture the most complex foraging tools used by nonhuman animals. Not only do they shape multiple tool designs of different complexity out of raw material using distinct, design-specific manufacture techniques, they are the only species to incorporate hook technology. The three different hook tool designs that they cut out of barbed *Pandanus* spp. leaves are suggested to have evolved by a process of diversification through cumulative changes rather than independent invention. Here, I describe three examples of an oversized version of the so-called 'narrow' pandanus tool design in an area where narrow tools are also made. My observation of the way a crow used one of these oversized tools in the wild suggests that they may be efficient for foraging in especially deep probe sites. The co-occurrence of two different designs originating from a very similar manufacture technique is consistent with diversification. Furthermore, qualitative data suggest that shape variation in the three previously described pandanus tool designs might be associated with ecological function. These findings strengthen the possibility that pandanus tool designs are an example of rudimentary diversification developed in close association with functional requirements. *Received 16 May 2013. Accepted 5 November 2013.*

Key words: *Corvus moneduloides*, cumulative change, design diversification, New Caledonian Crow, pandanus tools, tool manufacture, tool use.

New Caledonian Crows (NC crow; *Corvus moneduloides*) manufacture complex foraging tools because they shape distinct tool designs out of raw material that incorporate hook technology (Hunt 1996, Hunt and Gray 2002, 2004a, b). One material that they use to do this is *Pandanus* spp. (screw pine) leaves. The crows manufacture three distinct hook-tool designs from the barbed edges of these leaves: wide tool, narrow tool and stepped tool designs (Hunt and Gray 2003). Variation in the shape of each design mostly exists between sites, with a high degree of shape consistency within individual sites (Hunt and Gray 2003). The shape variation within both the uniformly broad wide tool and narrow tool designs is mostly to do with tool length. More complex shape variation exists among stepped tools because the characteristics of the tapered edge vary as well as tool length (e.g., the number and spacing of steps).

The manufacture of a pandanus tool can be inferred from inspecting missing sections of leaf edge on *Pandanus* spp. trees. The shape of a pandanus tool precisely matches the shape of the missing leaf edge associated with its manufacture (this missing edge is usually referred to as a 'counterpart'; Hunt and Gray 2003). Identifying a counterpart of the completed manufacture of a pandanus tool is not always straightforward. Wide

---

[1] School of Psychology, University of Auckland, Private Bag 92019, Auckland, New Zealand; e-mail: grhunt10@hotmail.com