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## Defining Cavity-associated Interactions Between Red-cockaded Woodpeckers and Other Cavity-dependent Species: Interspecific Competition or Cavity Kleptoparasitism?

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The endangered Red-cockaded Woodpecker (*Picoides borealis*) is unique in that it excavates cavities for roosting and nesting exclusively in living pines. Other cavity-dependent species, particularly Red-bellied Woodpeckers (*Melanerpes carolinus*) and flying squirrels (*Glaucomys volans*), commonly usurp these cavities (Ligon 1970, Jackson 1978, Neal et al. 1992, Loeb 1993, Kappes

and Harris 1995). Generally, these interactions are considered to be a form of interspecific competition (Ligon 1970, Jackson 1978, Carter et al. 1983, Harlow and Lennartz 1983, Rudolph et al. 1990, Loeb 1993, Kappes and Harris 1995, Winkler et al. 1995). I argue here that the term interspecific competition is inappropriate for describing heterospecific usurpation of roost or nest cavities because rather than being reciprocally negative (-,-), the interaction is negative for Red-cockaded

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Woodpeckers and beneficial for the cavity usurper (-, +). I conclude that heterospecific usurpation of Red-cockaded Woodpecker cavities, and analogous interactions between other species of excavators and usurpers, are more appropriately described as cavity kleptoparasitism.

Many authors have noted that heterospecific usurpation and occupation of Red-cockaded Woodpecker cavities can have negative effects on survival and reproduction (Ligon 1970, 1971; Jackson 1978; Baker 1983; Carter et al. 1989; Rudolph et al. 1990; Walters 1990; Neal et al. 1992; Kappes and Harris 1995). Carter et al. (1989) and Rudolph et al. (1990) hypothesized that Red-cockaded Woodpeckers forced to roost in the open are more vulnerable to predators and inclement weather. In northern Florida, all 15 adults that roosted in the open during a 17-month period had been displaced from their roost cavities by heterospecific usurpers (14 by Red-bellied Woodpeckers and one by a flying squirrel; Kappes unpubl. data). Red-cockaded Woodpeckers also may expend considerable energy defending cavities against usurpers (Ligon 1970), and displaced birds must reactivate existing cavities or excavate new ones; such activities during the breeding season may reduce fitness by diminishing time spent foraging and caring for young (Martin 1986). Additionally, the occupation of surplus Red-cockaded Woodpecker cavities by other species can preempt the use of these sites by adult Red-cockaded Woodpeckers whose original cavities become unsuitable, or by fledglings upon their departure from the nest. Moreover, cavity usurpers could prevent reproduction by occupying the only suitable cavities (Jackson 1978, Harlow and Lennartz 1983), and can injure or kill adult Red-cockaded Woodpeckers (Ligon 1971, Neal et al. 1992). LaBranche and Walters (1994) concluded that heterospecific cavity nesters destroyed more Red-cockaded Woodpecker nests than did predators.

Previous reviews of the effects of these interactions (i.e. Carter et al. 1989; Rudolph et al. 1990; Walters 1990, 1991; Conner et al. 1996) concluded that the data needed to evaluate whether the interactions have population-level effects on Red-cockaded Woodpeckers (thereby constituting interspecific competition) are lacking. When considered at the level of the individual (Martin 1986), the negative effects of heterospecific usurpation of Red-cockaded Woodpecker cavities are more apparent. However, the question of whether competition acts at the level of the population or the individual is beyond the scope of this paper. Even if these interactions have population-level effects on Red-cockaded Woodpeckers, or, if one considers interspecific competition to be an individual-level process, the term interspecific competition remains inappropriate because competitive interactions require reciprocal negative effects on the species involved (MacArthur 1972).

Previous discussions have stressed how hetero-

specific usurpation of cavities can have negative effects on Red-cockaded Woodpeckers while ignoring the consequences of these interactions for cavity usurpers. Because the interaction between cavity usurpers and Red-cockaded Woodpeckers is negative for Red-cockaded Woodpeckers and beneficial for the usurpers (which are acquiring a limiting resource), the interaction is a form of non-trophic parasitism, or, more specifically, kleptoparasitism (Brockman and Barnard 1979, Grier and Burk 1992). Although the term kleptoparasitism generally is applied to the theft of food (Brockman and Barnard 1979, Furness 1987), here it is extended to the theft of spatial resources such as nest sites. Thus, I define cavity kleptoparasitism as the usurpation by one species of cavities excavated by individuals of another species. I suggest that cavity kleptoparasitism is an appropriate term for the interaction between Red-cockaded Woodpeckers and other species that usurp their cavities. Similarly, analogous interactions between other cavity excavators and cavity usurpers, which generally are referred to as interspecific competition (e.g. Troetschler 1976, Short 1979, Ingold 1994, Winkler et al. 1995), are more appropriately described as cavity kleptoparasitism.

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### Interspecific Aggression in *Formicarius* Antthrushes? The View from Central Amazonian Brazil

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Two species of terrestrial antbirds, the Black-faced Antthrush (*Formicarius analis*) and the Rufous-capped Antthrush (*F. colma*), are sympatric through much of

lowland Amazonia (Ridgely and Tudor 1994). In Manu National Park, in southeastern Peru, *F. analis* (58 g) is behaviorally dominant to the smaller *F. colma* (49 g; Robinson and Terborgh 1995). *Formicarius analis* also is much more common and has smaller territories. Robinson and Terborgh suggested that the coexistence of

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