Geographic and ontogenetic variation in the contact calls of the kea (Nestor notabilis)

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Summary
Regional and ontogenetic variation in the contact calls of the kea (Nestor notabilis), an omnivorous and socially complex New Zealand parrot, were examined throughout the range of the species. We recorded samples of kee-ah contact calls from sixteen resident adults and eleven juveniles and demonstrated significant differences between age classes in the acoustic form of the vocalization. Canonical correlation analysis revealed a gradient in the form of the kee-ah call in both adults and juveniles along and across the escarpment of the Southern Alps, the primary longitudinal mountain range on the South Island of New Zealand. Although the juvenile call varies geographically along the same axes as the adult version, the aspects of the call that vary geographically are strikingly different, suggesting that the variation results from independent processes of vocal learning in the two age classes. A similar analysis of squeal vocalizations, which are only produced by juveniles, found even greater levels of geographic variation. We suggest that the immediate social environment may serve as the primary factor shaping the vocal patterns of both juveniles and adults, producing localized homogeneity in call form within each age class.

Keywords: Psittaciformes, Aves, vocal communication, ontogeny, development, regional dialects.

Introduction
Studies of the vocal behavior of wild parrots can provide a novel perspective on the adaptive significance of vocal communication in birds. Unlike many passerines, vocal learning in parrots is not generally restricted to early stages
of development; vocalizations in many species remain plastic throughout
life, susceptible to modification or augmentation in response to social influ-
ences (Nottebohm, 1970; Farabaugh & Dooling, 1996; Brown & Farabaugh,
1997; Hile et al., 2000). Vocal mimicry, both intra- and interspecific, also
appears to be far more common in parrots than in songbirds (Kroodsma &
Baylis, 1982; Rowley & Chapman, 1986; Cruickshank et al., 1993). The
neurological bases for vocal control and vocal learning in parrots differ sig-
nificantly from those in songbirds (Ball, 1994; Striedter, 1994; Brenowitz,
1997), suggesting that vocal cognition has evolved independently in the two
groups and may serve substantially different functions (Nottebohm, 1972).

Research on the vocal communication of parrots, particularly among wild
birds, has been very limited, however (Baker, 2000, 2001; Bradbury, 2003).
Of the more than 350 species of parrots (Juniper & Parr, 1998), the vocal
behavior of less than a dozen has been systematically investigated in the
field (e.g. Brereton & Pidgeon, 1966; Pidgeon, 1981; Martella & Bucher,
1990; McFarland, 1991; Fernández-Juricic et al., 1998; Fernández-Juricic
& Martella, 2000; Venuto et al., 2000; Wirminghaus et al., 2000). Previous
studies of parrot vocalizations show marked variation both between indi-
viduals and across geographic regions. Evidence for individual discrimina-
tion of contact calls has been shown in spectacled parrotlets (Forpus con-
spicillatus; Wanker & Fischer, 2001), white-tailed black cockatoos (Calyp-
torhynchus funereus; Saunders, 1983), galahs (Cacatua roseicapilla; Row-
ley, 1980), and budgerigars (Melopsittacus undulatus; Ito & Mori, 1999). Re-
gional variation in the acoustic form of specific call types has been described
in yellow-naped Amazons (Amazonia auropalliata; Wright, 1996; Wright
& Wilkinson, 2001), orange-fronted conures (Aratinga canicularis; Brad-
bury et al., 2001), ringnecked parrots (Bernardius zonarius; Baker, 2000)
and galahs (Baker, 2003). In several of these species, playback studies have
subsequently demonstrated differential responding to local and distant di-
alects (Wright & Dorin, 2001; Vehrencamp et al., 2003).

Many parrots have a relatively prolonged juvenile phase, entailing per-
sistent structured associations among young birds (Stamps et al., 1990;
Garnetzke-Stollman & Franck, 1991; Munn, 1992; Wanker et al., 1996,
1998; Diamond & Bond, 1999, 2003). In species with an extended juve-
nile period and identifiable morphological and behavioral stages, we might
expect to find evidence of juvenile vocalizations that are not just approxima-
tions to adult calls, but that exhibit their own characteristic acoustic forms