Sex biased natal dispersal is not a fixed trait in a stable population of Seychelles warblers

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(Accepted: 12 May 2010)

Summary
We observed a change in the sex-specific rate of delayed natal dispersal in a stable population of Seychelles warblers over a period of 20 years. At first, females were more likely to delay dispersal in their first year of life than were males, whereas later there was no sex bias in the rate of delayed natal dispersal. Similarly, the female-bias in helping-at-the-nest and the male-bias in floating have also weakened over time. These changes may have resulted from the decrease in variation in territory quality observed in the population over the study period. Our findings strengthen the view that natal dispersal is a highly plastic response to local ecological and social circumstances, and clearly show that rates of sex-biased dispersal cannot be considered a species or population constant. Our study also highlights the importance of collecting long-term datasets to understand complex behaviour such as natal dispersal.

Keywords: natal dispersal, sex bias, territory quality, habitat change, sex ratio, Acrocephalus sechellensis, delayed dispersal.

Introduction
Group living occurs in a wide range of taxa and often results from delayed dispersal of independent offspring (Emlen, 1995). Although both sexes may

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delay their dispersal, one of the sexes generally is more prone to disperse or to disperse earlier in life than the other sex (reviewed in Greenwood, 1980; Clarke et al., 1997). This sex bias in dispersal rate has been related to processes such as inbreeding avoidance, local resource and local mate competition (Greenwood, 1980; Dobson, 1982; Pusey, 1987), and local kin cooperation (Perrin & Lehmann, 2001; Le Galliard et al., 2006). Numerous studies have investigated natal dispersal in many different species and many of those report sex-biased dispersal. This seems to suggest that a sex bias in delayed natal dispersal is a species or population constant. However, delayed natal dispersal may probably best be viewed as a plastic response to local ecological and social conditions (Clobert et al., 2001, 2004; Baglione et al., 2006; Handley & Perrin, 2007). When changes in the local environment elicit different responses from the sexes, such changes could alter the strength or even the direction of sex biased natal dispersal. Therefore, it is not unlikely that, for some species, the direction of sex biased delayed natal dispersal in a population varies over time.

Several field experiments support the idea that whether or not offspring delay their dispersal depends on local ecological and social conditions. For example, after transfer of carrion crow (Corvus corone corone) eggs from a non-cooperative colony in which offspring do not delay dispersal to a cooperative colony, most juveniles that hatched from the transplanted eggs delayed dispersal (Baglione et al., 2002). Similarly, in two newly founded populations of Seychelles warblers (Acrocephalus sechellensis) the length of time by which dispersal was delayed increased with increasing population size (Komdeur, 1992; Komdeur et al., 1995). There now also are suggestions that, in a stable population of Seychelles warblers, the initially observed sex-bias in delayed dispersal has disappeared, possibly because the sexes have responded differently to changes in the local environment. Using data collected in the Cousin Island population from 1985 to 1994, Komdeur (1996) showed that the higher the quality (in terms of food availability) of the natal territory, the longer independent offspring delayed dispersal. Because females were usually born on higher quality territories than males (Komdeur et al., 1997), females delayed dispersal longer than males (Komdeur, 1996). However, a study in the same population between 1995 and 2005 revealed that during this period males were just as likely to delay dispersal in their first year of life as were females (Eikenaar et al., 2007). Furthermore, the