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More daughters in a less favourable world: Breeding in intensively-managed orchards affects tertiary sex-ratio in the great tit

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Abstract

Offspring sex-ratio is a key life-history trait that shows considerable variation among many bird species. Habitat quality is one of the numerous environmental factors acting on bias in sex-ratios in passerines. For the great tit *Parus major*, southern French apple orchards constitute both feeding and breeding habitats of considerably varying quality depending on the annual amount of chemical pesticides used for pest control, which have both direct (toxicity) and indirect (lower prey availability) effects on bird populations. In a two-year study, we specifically assessed the effect of three pest management strategies involving high (conventional), moderate (IPM) and no (organic) chemical pesticide inputs on fledgling sex-ratio using molecular sexing techniques. We found that great tit populations had significant variations in fledgling sex-ratio across our range of habitat quality, with conventional apple orchards producing a more biased sex-ratio towards daughters than IPM and organic orchards. Estimates of maternal traits (female body condition, first egg-laying date, clutch size and hatching rate) were also analysed but they were not significant predictors of brood sex-ratio. This study supports the sensitivity of bird tertiary sex-ratio to habitat quality. It also suggests that highly pesticide-treated agro-ecosystems may be poorer habitats for temperate insectivorous bird species. We provide further evidence that reducing chemical pressure might mitigate anthropogenic impacts on bird life-histories and population dynamics.

Zusammenfassung

Das Geschlechterverhältnis des Nachwuchses ist ein Schlüsselmerkmal der Lebensgeschichte, welches beträchtlich zwischen Vogelarten variiert. Die Lebensraumqualität ist einer der zahlreichen Umweltfaktoren, die auf das Geschlechterverhältnis von Singvögeln einwirkt. Für die Kohlmeise (*Parus major*) bilden Apfelplantagen im Süden Frankreichs Nahrungs- und Bruthabitate von unterschiedlicher Qualität, welche von der Jahresmenge der eingesetzten Pestizide abhängt, die sowohl direkte (Toxizität) und indirekte (geringere Beuteverfügbarkeit) Auswirkungen auf Vogelpopulationen haben. In einer zweijährigen Studie bestimmten wir den Einfluss von drei Managementstrategien zur Schädlingskontrolle, die hohen (konventionell), mittleren

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(integriert) bzw. keinen (biologisch) Einsatz von chemischen Pestiziden beinhalteten, auf das Geschlechterverhältnis der Küken, wobei wir das Geschlecht molekular bestimmten. Wir fanden, dass Kohlmeisenpopulationen über unseren Bereich von Habitatqualität hinweg signifikante Unterschiede hinsichtlich des Geschlechterverhältnisses der Küken aufweisen können, wobei konventionelle Apfelplantagen ein stärker zu Töchtern hin verschobenes Geschlechterverhältnis hervorbrachten als integrierte und biologische Plantagen. Messungen von mütterlichen Merkmalen (körperliche Verfassung der Weibchen, Tag der ersten Eiablage, Gelegegröße und Schlüpfrate) wurden ebenfalls analysiert, aber sie steuerten das Geschlechterverhältnis der Nachkommen nicht signifikant. Diese Studie bestätigt die Empfindlichkeit des tertiären Geschlechterverhältnisses bei Vögeln gegenüber der Habitatqualität. Sie legt ebenfalls nahe, dass stark mit Pestiziden behandelte Agrarökosysteme schlechtere Habitate für insektenfressende Vögel sein können. Wir erbringen desweiteren Belege dafür, dass eine Reduktion der chemischen Belastung den anthropogenen Einfluss auf die Lebensgeschichte und Populationsdynamik von Vögeln abschwächen könnte.

Keywords: Agro-ecosystem; Fledgling sex-ratio; Habitat quality; *Parus major*; Pesticides

Introduction

Variation in offspring sex-ratio, the relative number of sons and daughters, is a key enigma in population biology since it is a major component of species life-histories and population dynamics. Sex allocation theory is well defined (Fisher 1930; Trivers & Willard 1973) but its empirical support in vertebrates is still ambiguous. Many studies that provided evidence of bias in sex-ratio raised the critical question of the adaptive significance of such departures from the expected parity model (Clutton-Brock, Albon, & Guinness 1985; West & Sheldon 2002), and the underlying mechanisms of sex allocation are not fully understood as many studies also find no or opposing patterns (Pen & Weissing 2000; Komdeur & Pen 2002). In birds, almost half of all orders contain species with apparent ability of parents to manipulate the sex of their offspring either at the pre-ovulation or at both the post-ovulation and post-hatching period (Kilner 1998; Pike & Petrie 2003; Badyaev et al. 2005). Sex allocation in sexually dimorphic and monomorphic bird species can display facultative adjustments of primary and/or secondary sex-ratios that are expected in both cases to maximize parental fitness by skewing offspring sex-ratio towards the more beneficial sex under local prevailing circumstances (Trivers & Willard 1973; Gowaty 1993; Komdeur, Daan, Tinbergen, & Mateman 1997; Nager, Monaghan, Griffiths, Houston, & Dawson 1999; Rosivall, Szöllösi, Hasselquist, & Török 2010).

Biased brood sex-ratio in birds is generally viewed as an adaptive response to numerous factors acting at different scales and differing greatly between species (Komdeur & Pen 2002). These factors comprise variations in prey abundance (Appelby, Petty, Blakey, Rainey, & MacDonald 1997), weather conditions (Burley, Zann, Tiddeman, & Male 1989; Stauss, Segelbacher, Tomiuk, & Bachmann 2005), clutch size (Dijkstra, Daan, & Pen 1998), diet (Bradbury & Blakey 1998), or male attractiveness (Yamaguchi, Kawano, Eguchi, & Yahara 2004) or body size (Kölliker et al. 1999) and parental condition (Nager, Monaghan, Houston, & Genovart 2000; Stauss, Segelbacher, et al. 2005). Sex allocation is also sensitive to habitat quality, with high-quality territories producing broods biased towards sons and poor-quality territories producing broods biased towards daughters in passerine birds (Suorsa et al. 2003; Bell, Owens, & Lord 2014). Assessing the role of habitat quality on variation in sex-ratio implies that critical habitat characteristics can be clearly identified or, ideally, experimentally manipulated to demonstrate causal relationships between sex-ratio variation and environmental properties (Lessells, Oddie, & Mateman 1998; Komdeur & Pen 2002). In this regard, agro-ecosystems represent an ideal setting. First, human-made changes in the environment are generally assessable. Second, such changes increase temporal unpredictability in the environmental conditions during the breeding season, which impairs habitat quality for birds (Robinson & Sutherland 2002). For instance, the use of chemical pesticides is one well-known anthropogenic pressure that affects life-histories of insectivorous birds through direct toxic effects (including lethal effects) from dermal contact with chemicals and/or ingestion of contaminated food (Brewer, McQuillen, Mayes, Stafford, & Tank 2003), and through indirect resource effects resulting from drastic reductions of food availability (Sauphanor & Audemard 1983; Genghini, Gellini, & Gustin 2002). Consequently, such intensively-managed ecosystems allow considering identifiable ecological factors that may be involved in biases at the tertiary sex-ratio level (i.e. at fledging).

The overall aim of this study was to focus on the interactions between habitat quality and tertiary sex-ratio in wild populations of the great tit (*Parus major*) that use commercial orchards for both feeding and breeding. This common insectivorous passerine is considered a major model species in evolutionary ecology as it has been the subject of continuing long-term, individual-based field studies (Clutton-Brock & Sheldon 2010) and of both extensive phenotypic and genotypic characterization (Santure, Gratten, Mossman, Sheldon, & Slate 2011). The great tit has also become one of the most studied wild bird species as its