10

Genotype-by-Environment Interactions and Reliable Signaling of Male Quality in Bank Voles

Suzanne C. Mills, Mikael Mokkonen, Esa Koskela, and Tapio Mappes
Department of Biological and Environmental Science, University of Jyväskylä, Finland

10.1 Introduction

A male's heritable viability is often advertised through sexual signals (Fisher, 1930; Zahavi, 1975; 1977) whose reliability is likely maintained via resource allocation trade-offs (Gustafsson *et al.*, 1995, Moller & de Lope, 1995). Consistent with this, males with larger ornaments or weapons, greater body size, or higher rates of courtship showed greater survivorship or longevity (Jennions *et al.*, 2001). Positive relationships between a signal and viability are thought to be due to condition-dependent (a male's state prior to signal development) expression of sexual signals (Bonduriansky & Rowe, 2005; Kokko & Heubel, 2008; Radwan *et al.*, 2006; Tomkins *et al.*, 2004; Zahavi, 1977). However, male viability and condition also depend on the environment and a male's signal is only reliable when the signal/viability phenotypic correlation remains consistent across environments (Greenfield & Rodriguez, 2004). Spatial or temporal environmental heterogeneity can result in genotype by environment interactions (GEI) which result in some sexual traits performing optimally in certain environments, whereas other genotypes excel in different environments (reviewed by Bussiere *et al.*, 2008; Ingleby *et al.*, 2010) as exemplified by research on the lesser waxmoth, *Achroia grisella* (Danielson-Francois *et al.*, 2006; 2009;

Genotype-by-Environment Interactions and Sexual Selection, First Edition.
Edited by John Hunt and David Hosken.

Companion Website: www.wiley.com/go/hunt/genotype

Greenfield & Rodriguez, 2004; Greenfield *et al.*, 2012; Jia *et al.*, 2000; Rodriguez & Greenfield, 2003; Zhou *et al.*, 2008). Furthermore, if the reaction norms of different genotypes cross, such that the genotype with higher values in one environment has values lower than other genotypes in other environments (Roff, 1997), the relative fitness ranking of genotypes may change across environments (Fry, 1996; Gillespie & Turelli, 1989). These reaction norm crossovers likely occur as a female may still show a preference for superior males, but the preferred signal has transferred to another genotype. Thus, selection favors different genotypes in different environments. As there is a heritable component to both the male signal and the female preference for it (Hoffmann, 1991; Houde, 1992, and reviewed by, e.g., Bakker & Pomiankowski, 1995; Kokko *et al.*, 2003), a genetic correlation between the male signal and female mate preference will likely have been generated by linkage disequilibrium accrued during non-random mating (Fisher, 1930). In the case of crossing reaction norms, although the male's signal and heritable viability would remain the same, the genotype would not be paired assortatively with a female's preference, thereby breaking built up linkage and reducing genetic covariance between the signal and preference traits in the population (Greenfield & Rodriguez, 2004; Jia *et al.*, 2000). Such an outcome would have significant consequences for the overall strength of sexual selection.

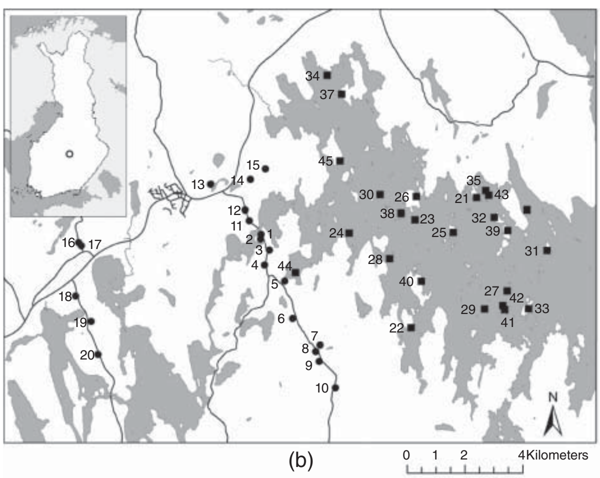
In this chapter, we introduce the bank vole, *Myodes glareolus,* and describe the environmental fluctuations to which the species is subjected. We then outline its mating system, the heritability and reliability of male signals and intralocus sexual conflict. We will then describe the presence of GEI for male dominance and highlight the impacts of signal unreliability in terms of the evolution of female mate preference, and the genetic covariance between the signal and preference. Finally, we discuss various mechanisms that might mitigate these impacts.

10.2 The bank vole

The bank vole, *Myodes glareolus,* (Figure 10.1a/Plate 6) is a common northern European rodent (Stenseth, 1985), which inhabits forests and fields, feeding mostly on plants, seeds, fungi, and even invertebrates (Hansson, 1985). The life-history pattern of the bank vole is characterized by a young age at maturation (Mappes & Koskela, 2004; Oksanen *et al.*, 2007), and a short lifespan of only three to five months on average (Innes & Millar, 1994) where only a fraction of individuals survive over one winter (Macdonald, 2001; Ostfeld, 1985; Prévot-Julliard *et al.*, 1999).

A bank vole's survival is compromised by multiple factors including ecto- and endoparasites, disease, starvation, and predation (Kallio *et al.*, 2007; Norrdahl & Korpimäki, 1995; Soveri *et al.*, 2000). For instance, Puumala Hantavirus, *Ixodes*-tick transmitted pathogens, helminthes, and coccidiosis are all pathogens that compromise bank vole survival (Hakkarainen *et al.*, 2007; Haukisalmi & Henttonen, 2000; Kallio *et al.*, 2007; Soveri *et al.*, 2000). Genetic disease resistance and immune response therefore have important consequences for survival and thus, fitness in this species.

(a)



(b)

Fig. 10.1 (a) The study species, the bank vole, *Myodes glareolus.* (Source: Photo by and reproduced with permission of Heikki Helle.) For color details, please see Plate 6. (b) The study area, Konnesvesi, is shown with a circle in the inserted picture of Finland in Scandinavia. The main map shows the vole trapping locations. Locations 1–20 (marked with circles) are the mainland sampling sites, and locations 21–45 (marked with rectangles) are the island sampling sites. This figure has been reproduced with permission from Rikalainen *et al.* (manuscript in prep). (c) The trapping index of bank voles in Central Finland during 1996–2009 (trapping index = captured individuals/100 trap nights, monthly data are interpolated from the trappings carried out four times per year, trappings are indicated with diamonds). The six analyzed cycle phases are indicated with light (peak years) and dark (crash years) bars. (Source: Rikalainen et al. 2012. © Rikalainen et al./CC-BY-SA-3.0.)

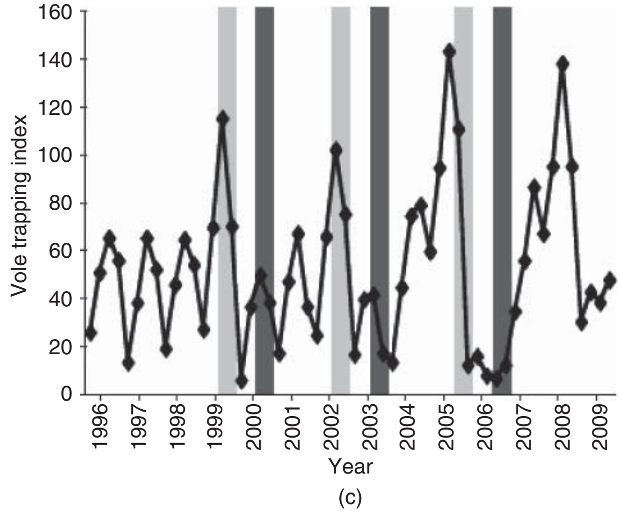


Fig. 10.1 (*continued*)

10.2.1 Environmental heterogeneity

Popularized by lemming populations (Elton, 1924), small mammals are renowned for the density dependent oscillations in their numbers (Krebs & Myers, 1974). A time-series study of a bank vole population covering approximately 100 km^2, has been carried out in Konnevesi, Central Finland (62°37'N, 26°20'E) since 1996 (Kallio *et al.*, 2009) (Figure 10.1b). The size of this population oscillated in three successive cycles with three density peaks and crashes during the years 1996–2009 (Figure 10.1c) (Rikalainen *et al.*, 2012). In addition to these 3–4 year cycles, bank voles experience annual/seasonal density cycles, which peak in the summer or autumn and crash in the spring (Koivula *et al.*, 2003). These seasonal and multi-annual cyclic fluctuations in population density cause temporal environmental heterogeneity (i.e., temporally varying selection, e.g., Roff, 1997) that are predicted to favor different alleles (and possibly further, even different genotypes, Chitty, 1967), during different phases of the population cycle (Mappes *et al.*, 2008a). The density-related changes faced by individual voles in their environment during their lifetime, including availability of food resources, free breeding territories, and pathogen pressure, have been found to affect multiple vole life-history traits (e.g., Beckerman *et al.*, 2002; Huitu *et al.*, 2003; 2007; Koskela *et al.*, 1998; Prévot-Julliard *et al.*, 1999; Soveri *et al.*, 2000, see, however, Eccard & Ylonen, 2001).

10.2.2 Female reproductive success

Bank voles have a high fecundity (1–10 pups per litter, average = 4.4–5.6 pups; Koivula *et al.*, 2003; Mappes & Koskela, 2004; Schroderus *et al.*, 2012), short gestation period (3 weeks), and they typically breed in post-partum estrus, resulting in up to four breeding events within the same reproductive season (Koivula *et al.*, 2003). In Central Finland, reproduction occurs from May until mid-September (Koivula *et al.*, 2003), and the first cohorts of the breeding season reproduce during their first year (Mappes *et al.*, 1995b), whilst late summer cohorts usually delay reproduction until the following breeding season. Therefore, successful overwintering is crucial for their fitness (Prévot-Julliard *et al.*, 1999).

Competition between territorial bank vole females is a major mechanism determining their breeding success, which, especially at high densities, leads to large variation in the relative fitness of individuals (Jonsson *et al.*, 2002; Koskela *et al.*, 1999; Oksanen *et al.*, 2007). Together, these selective environments could facilitate the origin and existence of alternative behavioral (Mappes *et al.*, 2012; Tuomi *et al.*, 1997) or life-history tactics (Kaitala *et al.*, 1997; Mappes *et al.*, 2008b) whose success would depend both on the current environment and the frequency of alternative life-history tactics in the population. Negative frequency-dependent and density-dependent selection on different breeding tactics in bank voles suggest that females with low reproductive effort (RE) are favored at low densities (e.g., after a population crash), whereas females with high RE are most successful when rare in high density populations (e.g., peak years) (Mappes *et al.*, 2008b).

10.2.3 Male signals, heritability, and reliability

Males provide no material resources to the females or offspring (Mazurkiewicz, 1971). Males do not express elaborate ornaments. Instead, direct male–male competition for sexually receptive females is one of the major mechanisms of sexual selection in the bank vole (Hoffmeyer, 1982; Oksanen *et al.*, 1999). In a similar manner to mice, olfactory signaling is also an important sexual signal in bank voles (Fischer *et al.*, 2003; Gosling & Roberts, 2001). Preputial gland products, mixed with urine during scent-marking (Brown & Williams, 1972), are the source of bank vole sex-attractants (Kruczek, 1994). Males use urine to both signal their dominance in male-male competition (Brinck & Hoffmeyer, 1974), and to advertise their social status to females who show preferences for dominant males (Horne & Ylönen, 1996, Klemme *et al.*, 2006a,2006b; 2012) and with large preputial glands (Kruczek, 1997).

Due to their short lifespan, reproductive success in the field can be interpreted as male fitness, and correlates with plasma testosterone (T) levels (Mills *et al.*, 2007b), as does male dominance in the laboratory (Box 10.1) (Mills *et al.*, 2007a). Exogenous T implants increased dominance in the laboratory, and increased home ranges and reproductive success in semi-natural populations (Mills *et al.*, 2009). Male bank voles show a steep Bateman gradient resulting in persistent directional sexual selection for increased mating success and increased T (Mills *et al.*, 2007b). Furthermore, the preputial gland is also T-dependent (Radwan *et al.*, 2006), therefore, strong selection on T will affect male mating success through its influence on both intra- and inter-sexual selection. T also plays an important role in spermatogenesis (mice and rats, Singh & Handelsman, 1996; Spaliviero *et al.*, 2004; Sriraman *et al.*, 2004), therefore it may also be acting on internal male reproductive traits such as sperm characteristics. Owing to overlapping insemination in this polygynandrous mating system, with up to three fathers siring litters at male-biased sex ratios (Klemme *et al.*, 2008; Mills *et al.*, 2007b), male–male competition may therefore be as intense at the ejaculate, as at the population level (Klemme & Firman, 2013).

Box 10.1 Measuring male bank vole dominance

Male mating success was measured in the laboratory in which two males and one female in estrus were released into an arena (1 × 1m) and observations made until ejaculation occurred (Oksanen *et al.*, 1999). In addition to urine marking and defecation, males indicate either aggressive or defensive behaviors within 5 min. Normally the aggressive male then courted the female with successful copulation once the female performed lordosis, whereas the other male retreated to the arena corner. Escalated male aggression only occurred when both males attempted to court the female. The male that successfully mated was considered dominant. Since the success of each male is dependent on the dominance of the other males allotted as his opponents, we corrected the initial dominance score (proportion of contests won) by the success of the opponents. Initial scores were corrected using the equation derived from Alatalo *et al.* (1991),

$$Q = F\mathrm{n}_F/[F\mathrm{n}_F + (1 - S)\,\mathrm{n}_S],$$

Q is the corrected dominance estimate, F and S are the mean uncorrected initial dominance scores of the opponents who either failed to copulate (F) or copulated successfully (S); n_F and n_S are the number of unsuccessful and successful opponents respectively. In this way, the corrected dominance estimate of males that beat successful opponents will increase, whereas the corrected dominance estimate of males that lost to less successful males will be reduced.

However, tight linkage between two immunological traits and male T level in the bank vole indicates that selection for higher T level in males will compromise the function of the immune system in both sexes (Schroderus *et al.*, 2010). Therefore, the reliability of dominance advertisement is not only enforced through social costs during competition, but also via a trade-off with immune response (Box 10.2: Mills *et al.*, 2009; 2010). Furthermore, energetic costs associated with investment in olfactory signaling were found in male bank voles suggesting that olfactory signaling is also a reliable indicator of male quality (Radwan *et al.*, 2006).

Box 10.2 Measuring the immune response in bank voles

An effective method for measuring the immune system is problematic due to the large number of interrelated immune components, as unexpected negative or positive correlations might arise when only a single immune measure is measured (Norris & Evans, 2000; Zuk & Stoehr, 2002). Therefore, we have developed three measures in the bank vole.

Firstly, circulating immunoglobulin G (total IgG level) was developed in the bank vole (Oksanen *et al.*, 2003). Total IgG level is one measure of the innate immune system, a vole's first line of defense against pathogens that aims to neutralize pathogens before a specific immune response is triggered, representing a state of immunological readiness (Greives *et al.*, 2006).

Secondly, by experimentally challenging the immune system with novel antigens and measuring concomitant host specific antibody titers against these antigens, one gets a good estimate of host resistance to a variety of pathogens (Hasselquist *et al.*, 1999; Svensson & Skarstein, 1997; Svensson *et al.*, 1998). A measure of humoral adaptive immunity, anti-bovine gamma globulin (BGG) antibody production (reflecting the resources put into the production of specific antibodies in response to the novel antigen injected, BGG), was established in the bank vole (Mills *et al.*, 2009; Oksanen *et al.*, 2003).

Thirdly, cell mediated adaptive immunity was assessed using a delayed-type hypersensitivity (DTH) test, a standard assay in veterinary medicine (Lochmiller *et al.*, 1993; Luster *et al.*, 1993). Phytohemagglutinin (200 μg PHA-P, lectin from red kidney bean, *Phaseolus vulgaris*) was injected into each footpad and the DTH-index was calculated as the difference in swelling between the control and the PHA as a percentage of mean footpad (Mills *et al.*, 2010).

Male bank vole T level shows moderate heritability (Mills *et al.*, 2009) suggesting a rapid evolutionary response to selection on it, and heritabilities of dominance-related traits, as well as male mating success, have been shown to be quite high in the bank vole (Horne & Ylönen, 1998; Oksanen *et al.*, 1999). Therefore, in a natural bank vole population with its plethora of parasites and pathogens, dominant males, with no visual signs of disease, have to have signaling viability that will be passed on to their offspring.

10.2.4 Intralocus sexual conflict

Testosterone is clearly essential for male bank vole reproductive behavior, however, if high T level had negative effects on female fitness, this would result in a sexually antagonistic hormone expression profile, unless selection has decoupled male and female T levels (Mank, 2007). When males and females differ in their optima for a morphological, physiological, or behavioral trait that has a strong intersexual genetic correlation, the alleles of the underlying polymorphic genes are beneficial to one sex but detrimental to the other, and an intralocus conflict is borne (Bonduriansky & Chenoweth, 2009; Chippindale *et al*., 2001; Lande, 1980; Rice, 1984; Westneat and Sih, 2009). Intralocus conflict has the potential to generate sexually antagonistic selection affecting important evolutionary processes and has been found in bank voles (Mills *et al*., 2012; Mokkonen *et al*., 2011).

We created artificial selection lines divergent in one study for male T and in another for dominance and measured relative adult fitness using genetic paternity analyses and competition trials. We found sexually antagonistic effects in the bank vole as the reproductive fitness estimates of full siblings are negatively correlated (Figure 10.2a) (Mills *et al*., 2012; Mokkonen *et al*., 2011). In addition, a negative correlation on the fitness of opposite-sex progeny (father–daughter, mother–son) was found, such that high T sires produce sons with high fitness, whereas low T sires produce daughters with high fecundity (Figure 10.2b) (Mills *et al*., 2012). The specific alleles of intralocus sexual conflict are largely unknown, but we found that for bank vole fitness, sexually antagonistic selection is acting on circulating male T levels, and maintains the strategy of multiple mating in the bank vole (Mokkonen *et al*., 2012). Therefore, selection for dominant males produces dominant sons, but daughters with low fecundity, possibly due to non-optimal hormone (T) levels and/or resource

▶ **Fig. 10.2** (a) Intersexual regression of adult F_1 fitness between brothers and sisters (litter means); selection groups and controls are shown separately.

= Groups selected *for* and *against* male T (simple linear regression: $F_{1,19} = 9.447$, $p = 0.006$, $R^2 = 0.33$; $y = -0.863x + 0.329$)
= control groups (simple linear regression: $F_{1,30} = 1.085$, $p = 0.306$, $R^2 = 0.035$; $y = 0.221x - 0.004$)

This figure has been reproduced with permission from Mills, S.C., Koskela, E., & Mappes, T. (2012) Intralocus sexual conflict for fitness: sexually antagonistic alleles for testosterone. *Proceedings of the Royal Society B-Biological Sciences*, 279: 1889–1895.

(b) Mean (± SE) relative adult fitness between F_1 brothers and sisters from mixed sex litters.

= groups selected *for* male T (HiT/HiT), n = 13
= groups selected *against* male T (LoT/LoT), n = 8
X = control groups (mating between groups; HiT/LoT and LoT/HiT), n = 32

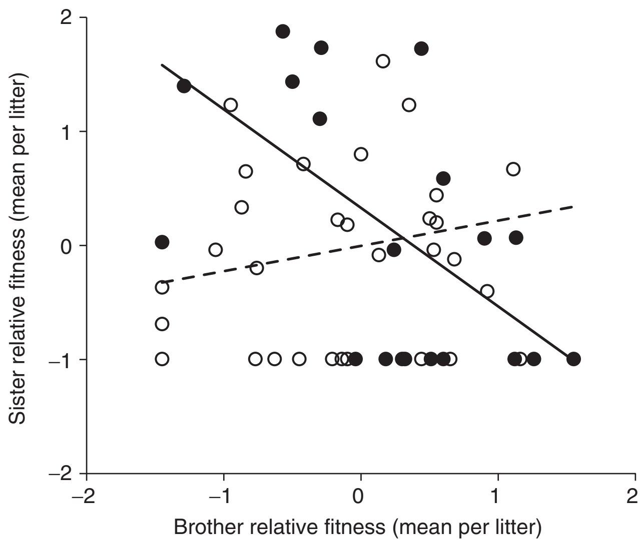
Sample size (n) refers to the number of litters including both sexes (means taken within a litter). Error bars indicate 1 standard error.

This figure has been reproduced with permission from Mills, S.C., Koskela, E., & Mappes, T. (2012) Intralocus sexual conflict for fitness: sexually antagonistic alleles for testosterone. *Proceedings of the Royal Society B-Biological Sciences*, 279: 1889–1895.

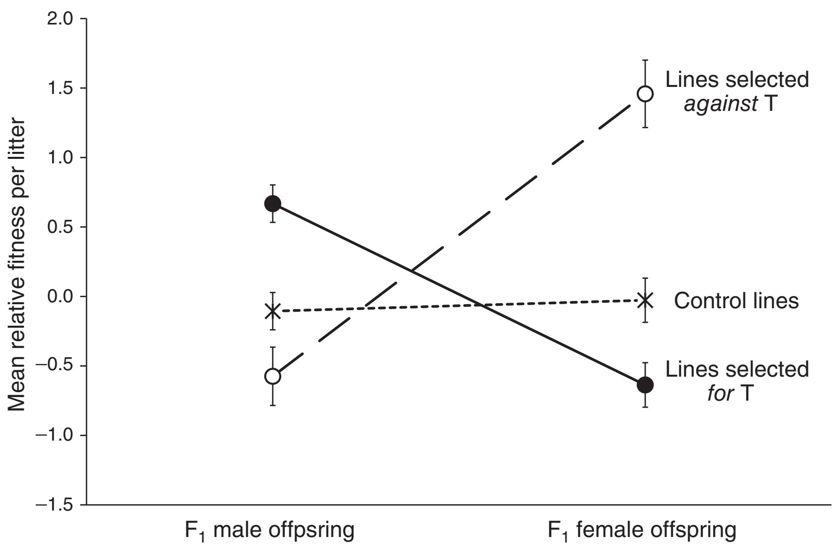
re-allocation affecting their fecundity. However, do dominant males produce dominant sons when the environment changes?

10.3 GEIs on male dominance in the bank vole

Vole life-history traits show strong plasticity, which may be highly advantageous in fluctuating environments (Ergon *et al.*, 2001a). Many traits from juvenile growth rate, female sexual maturation, T level and reproductive successes are



(a)



(b)

decreased or suppressed at high population density (Bujalska, 1985; Ergon *et al.*, 2001b; Koskela *et al.*, 1999; Kruczek & Marchlewska-Koj, A., 1986; Mappes *et al.*, 2008b; Oksanen *et al.*, 2007; Ostfeld & Canham, 1995; Prévot-Julliard *et al.*, 1999). Therefore, there is a strong possibility that the environment will have varying effects on different genotypes in the bank vole.

We investigated the effects of stable and changing rearing environments between father and son on the heritability and plasticity of male bank vole dominance (Mills *et al.*, 2007a). Male dominance was measured (Box 10.1) from all potential fathers, who were then mated with females. Litters were cross-fostered and rearing environmental density was manipulated (Box 10.3) such that full sibs were exposed to all three rearing environments (good, control, and poor, in terms of resource availability). Once sexually mature, dominance and plasma T levels were measured in male offspring and litter size was measured in female offspring.

Box 10.3 Cross-fostering and litter density manipulation

Male bank voles were randomly paired for a week with females. Upon parturition, pups were sexed, individually tagged, weighed and within two days of birth the litters were cross-fostered: a foster mother's litter was replaced with single pups from different donor mothers (Mappes *et al.*, 1995a; Mappes & Koskela, 2004). Cross-fostering excludes any confounding effects of possible variation in post-birth maternal quality. Previous studies found no differences between the growth and survival of fostered and non-fostered pups (Mappes *et al.*, 1995a).

Litter size was artificially manipulated by moving −2, ±0, and +2 pups to and from litters. The removal of two pups results in a greater amount of resources, such as milk, available per remaining pup, and represents a "good" rearing environment in nature. Although mothers increase their milk production after the addition of two pups, the amount received per pup is still lower than that received per pup in unmanipulated litters (Koskela *et al.*, 2009, Koskela, unpubl. data) and enlarging a litter can have detrimental effects on pup growth (Oksanen *et al.*, 2003). Thus, enlarged litter treatments represent "poor" rearing environments in nature, such as increased female-female competition at high population density or low food availability, where mothers would receive fewer resources and in turn provide less to their offspring (Koskela *et al.*, 1998). The manipulation of the rearing environment consisted of a foster mother's original litter being replaced with pups from donor mothers and took place at the same time as cross-fostering. Litter manipulations were carried out in relation to the foster mother's original litter size. Male and female offspring from a single sire were split between the three manipulated rearing environments.

Male dominance shows considerable plasticity across different environments (Figure 10.3a) (Mills *et al.*, 2007a). There was also a significant interaction between paternal dominance and the rearing environment on offspring dominance, which suggests that environmental effects on dominance differed among sons from different fathers (GEI). We found a significant crossing-over of reaction norms implying that none of the three paternal groups signal the highest dominance in all environments (Schlichting & Pigliucci, 1998). In good rearing environments, highly dominant fathers sire offspring of higher dominance than offspring of subordinate fathers. However, the situation is reversed in poor rearing environments in which dominant fathers produced subordinate offspring and dominant offspring are sired by subordinate fathers. Offspring of the high and low dominance paternal groups show the greatest plasticity in dominance, that is, the greatest response to environmental change. We also found considerable plasticity in male T levels across environments (Figure 10.3b). We found a GEI between paternal dominance and the rearing environment on offspring T levels, suggesting that, in agreement with dominance, environmental effects on T level differed among sons from different fathers (Figure 10.3b).

As predicted by Greenfield and Rodriguez (2004), GEI with crossing reaction norms has the potential to render signals unreliable and reduce the genetic benefits to females from mating with dominant males. In the bank vole, signal reliability, or the genetic benefit to females from mating with dominant males, depends on the stability of environments and the environment experienced by their offspring, rather than male quality per se. Therefore, the presence of GEI also impacts the evolution of female mate preference. Whilst, the heritability of female bank vole preferences has not been measured, male signals are heritable (Horne & Ylönen, 1998; Mills *et al.*, 2009; Oksanen *et al.*, 1999) and here we are assuming that there is genetic covariance between them. GEI in bank voles would thus result in the male genotype no longer being paired assortatively with a female's preference and eroding signal-preference covariance.

The next part of this chapter will discuss various mechanisms that might mitigate the effects of GEI on both the net direction of sexual selection and on the genetic covariance between the signal and preference. Firstly, if both the male signal and female preference traits had roughly parallel norms of reaction, signal reliability and genetic covariance would be maintained (Greenfield & Rodriguez, 2004). Secondly, if both alternative male strategies and female preferences were present and maintained by fluctuating selection and advantage of the rare male phenotypes. Finally, by sexual antagonism, whereby the production of daughters with high reproductive success compensates for the loss in son fitness.

10.4 Suggestions to reconcile the disruption of the signal-preference covariance

10.4.1 Parallel norms of reaction for male signal and female mate preference

The disruption of genetic covariance caused by GEI may be lessened by matching variation in the male and female traits (Rodriguez & Greenfield, 2003). If the reaction norm genotypes for female mate preference respond to environmental conditions in ways that mirror the responses of male signaling genotypes, then genetic covariance will be maintained (Greenfield *et al.*, 2012). Yet, despite its importance for sexual selection there have been relatively few investigations into genetic variation for preference, how sensitive female preferences are to the environment or more importantly, whether this preference varies with female genotype to generate GEI for preference (Ingleby *et al.*, 2010).

Plasticity in female mate preference has been found in the tungara frog, *Pysalaemus pustulosus* and the lark bunting, *Calamospiza melanocorys*, across breeding seasons (Chaine & Lyon, 2008; Lynch *et al.*, 2005). GEI for female preference functions and choosiness were found in *Drosophila melanogaster,* however, as yet these have not been compared with male reaction norms (Narraway *et al.*, 2010). Variation in female mate preferences have been shown to match seasonal or ecological variation in male parental care and growth rate in collared flycatchers and soil mites, respectively (Lesna & Sabelis, 1999, Qvarnstrom *et al.*, 2000), but it is not known whether their reaction norms match. In the lesser waxmoth, *A. grisella,* artificial selection on rearing temperature revealed phenotypic plasticity, GEI and ecological crossovers for female mate preference, but the reaction norms for preference pulse-thresholds in females do not match the reaction norms for male signals (Rodriguez & Greenfield, 2003). The authors predicted

▸ **Fig. 10.3** (a) Offspring dominance (mean $Q \pm 1$ SE; see Box 10.1) produced by the three paternal groups (based on dominance) across the different rearing environments.

—○— = low paternal dominance (*Q:* 0 - 0.2): y = 0.227x - 0.014, *n* = 31, *P* = 0.024
X - - - = medium paternal dominance (*Q:* 0.21 – 0.79): y = 0.06x + 0.31, *n* = 42, *P* = 0.343
—■— = high paternal dominance (*Q:* 0.8 – 1): y = –0.138x + 0.77, *n* = 41, *P* = 0.115.

A significant level of crossover between the high and middle paternal groups was identified (min (Q^+, Q^-) = 4.61, *I* = 3, $P < 0.05$).

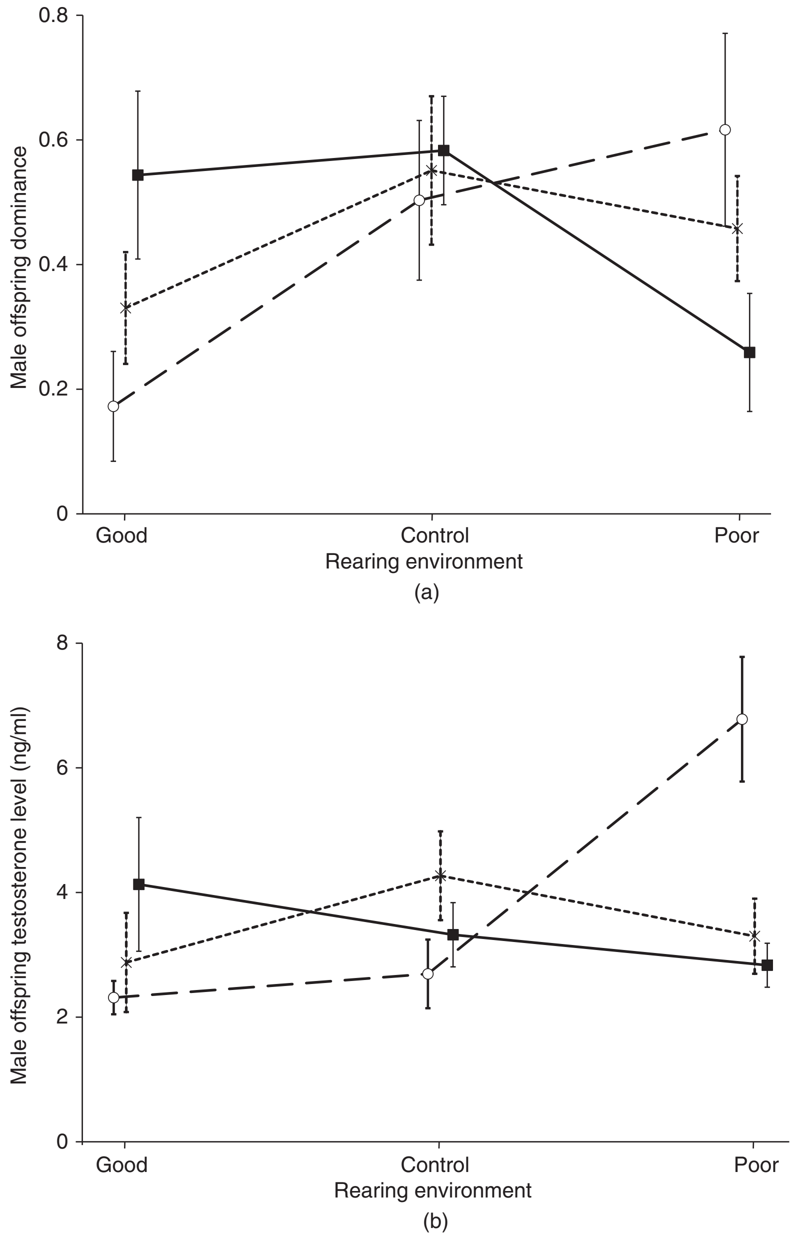
This figure has been reproduced with permission from Mills, S.C., Alatalo, R.V., Koskela, E., Mappes, J., Mappes, T., & Oksannen, T.A. (2007a) Signal reliability compromised by genotype by environment interaction and potential mechanisms for its preservation. *Evolution*, 61–67: 1748–1757.

(b) Offspring plasma testosterone level (mean ± 1 SE) produced by the three paternal groups (based on dominance) across the different rearing environments.

—○— = low paternal dominance (*Q:* 0 – 0.2): y = 2.199x – 1.08, *n* = 10, *P* = 0.079
X - - - = medium paternal dominance (*Q:* 0.21 – 0.79): y = 0.465x + 2.675, *n* = 11, *P* = 0.542
—■— = high paternal dominance (*Q:* 0.8 – 1): y = -0.923x + 5.281, *n* = 12, *P* = 0.083.

This figure has been reproduced with permission from Mills, S.C., Grapputo, A., Jokinen, I., Koskela, E., Mappes, T. & Poikonen, T. (2010) Fitness trade-offs mediated by immunosuppression costs in a small mammal. *Evolution*, 64, 166–179.

that the preference genotypes would not favor the same signal genotypes across environments (Rodriguez & Greenfield, 2003). Additionally, a 25-year study of a population of collared flycatchers found that females only received a fitness benefit, in terms of relative recruitment success, associated with choosing highly ornamented males during drier breeding seasons, with the opposite being true during the wettest breeding seasons (Robinson *et al.*, 2012). Furthermore, a lack



of covariance between female mate preference and male ornament, as well as low heritability of female choice in collared flycatchers has previously been found (Qvarnstrom *et al.*, 2006), suggesting that sexual selection within a population can be highly variable and dependent upon prevailing weather conditions (Robinson *et al.*, 2012). Therefore, the current evidence for matching female preferences with male signals across environments appears weak.

It would be interesting to measure whether female bank vole preference differs as a function of their rearing environment, as well as across stable and unpredictable environments. Theory predicts that the evolution of phenotypic plasticity depends upon the degree of spatial and temporal heterogeneity in the environment, which is clearly present in bank vole populations, as well as the presence of cues that reliably indicate future changes in the environment (Alpert & Simms, 2002; Hairston & Munns, 1984; Levins, 1968; Lively, 1986). In terms of multi-annual cycles, the cues that females could use to accurately predict future environmental conditions that her offspring would experience, could include population density tracking, for example via the concentrations of the stress hormone, corticosterone, that in some species increases with increasing territorial intrusions (Comendant *et al.*, 2003). In terms of seasonal density changes, females could use day length as a cue for the advancing winter. Therefore, cues are a possibility, however, for the reaction norms of female mate preference to match those of the male signal, female mate preference

▸ **Fig. 10.3 (continued)** (c) Relationship between three fitness-related life-history traits across immune groups. Fitness represents the reproductive success of males, which also incorporates mortality. Survival represents end of breeding season survival. Reproductive effort represents the ranked dominance of males measured in sterile laboratory conditions prior to the field experiment. All traits were made relative by dividing by the population mean and standardized to have a mean of 0 and standard deviation of 1. Sample sizes for fitness and survival = 112 and for reproductive effort = 56.

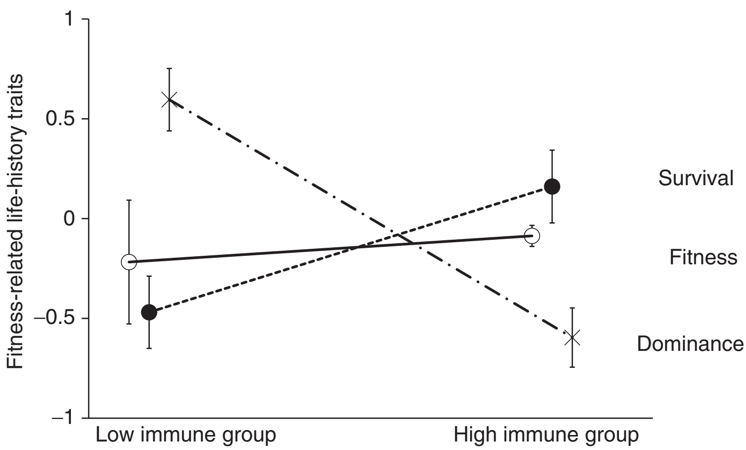
—○— = fitness (field reproductive success which also incorporates mortality)
▪●▪ = survival (alive or dead at the end of the breeding season)
▪▪▪▪▪ X = reproductive effort (high to low dominance ranked 4 to 1).

This figure has been reproduced with permission from Mills, S.C., Grapputo, A., Jokinen, I., Koskela, E., Mappes, T. & Poikonen, T. (2010) Fitness trade-offs mediated by immunosuppression costs in a small mammal. *Evolution*, 64, 166–179.

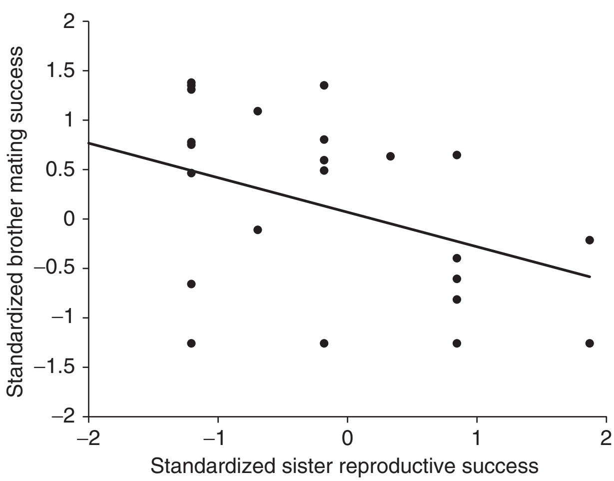
—●— (d) Fitness relationship between a brother's dominance and his sister's reproductive success (litter size) when reared in poor (enlarged litter) environments. Mating and reproductive successes were standardized for the whole population. $y = -0.35x + 0.087$, $n = 24$, $P = 0.045$, $R^2 = 0.17$.

This figure has been reproduced with permission from Mills, S.C., Alatalo, R.V., Koskela, E., Mappes, J., Mappes, T., & Oksannen, T.A. (2007a) Signal reliability compromised by genotype by environment interaction and potential mechanisms for its preservation. *Evolution*, 61–67: 1748–1757.

would need to be plastic and adaptive and currently this has not been tested. However, intra-sexual selection, via male-male competition, is still an important component of male mating success, and depends on current environmental conditions, rather than those in the future (Figure 10.3a). Therefore, whilst female mate preference may be plastic and change to adapt to future environmental conditions, male dominance cannot. Dominant males will still pass on genes that make their offspring more sensitive to poor conditions. Nevertheless, being a polygynandrous species (Mills *et al.*, 2007b), female bank voles with plastic mate preferences may be able to mate with some subordinate males. Such multiple matings, coupled with cryptic female choice (see Section 10.4.3), may still enable the female preference-male signal covariance to be passed on to at least some of her offspring. However, as female plastic mate preferences



(c)



(d)

would be unable to fully compensate for the behavior of dominant males, the strength of sexual selection will still be decreased.

10.4.2 Alternative strategies for male signal and female preferences

The presence of crossover interactions of reaction norms between paternal groups for male dominance in the bank vole (Figure 10.3a,b) suggests that there may be alternative male strategies in different environments (Mills *et al.*, 2007a). In addition, another study found differences in male dominance and mobility, as well as immune response and survival between bank voles groups with naturally high and low T levels, also advocating the presence of two alternative reproductive strategies (Mills *et al.*, 2009). Furthermore, the presence of genetic covariance between male T and male immune response (Schroderus *et al.*, 2010) coupled with the knowledge that males with divergent immune responses have equal fitness (Figure 10.3c) (Mills *et al.*, 2010), may also demonstrate the presence of evolutionary stable signaling strategies (ESS) for reproductive effort and survival (Mills *et al.*, 2010). However, future work should be carried out to verify these hypotheses.

Males from one strategy, high dominance, may sire attractive offspring that may have matured faster or have fed better in stable, favorable environments, but whose genes may be more sensitive when the rearing environment deteriorates from father to son. This may occur following an increase in population density (peak year), causing a decrease in available food or an increase in parasites; such offspring may not be able to afford the costs of dominance (Mills *et al.*, 2009). A second strategy, low dominance, may be unable to compete with dominant males in stable, favorable environments, however, males of low dominance may be less sensitive when rearing environments deteriorate and thus, may be able to bear the costs of dominance. We predict that variation in selection for immune-related traits (Schroderus *et al.*, 2010) during the multi-cyclic density fluctuations (Kallio *et al.*, 2009) might be driving these different male dominance strategies as pathogen pressure (Soveri *et al.*, 2000) and immunological parameters of voles (Huitu *et al.*, 2007) differ between peak and crash years. Males with low genetic resistance to disease (but high dominance) are only handicapped by reproductive effort when parasites were present (Mills *et al.*, 2010). Therefore, the increased susceptibility to disease during peak years of the population cycles may be driving the reduced fitness of sons sired by high dominance males in poor rearing environments.

If females show different mate preferences for the two alternative strategies (high and low dominance), which via non-random mating are linked to the two signals of each male strategy, then genetic covariance would not be weakened by GEI. But would such a preference for low dominance evolve when females only receive indirect benefits every 3–4 years at peak density? Kokko *et al.*, (2007) highlighted that preference for rare male phenotypes can aid preference evolution. In the bank voles, the majority of the time, the high dominance male strategy would be most common in the population, as high dominance males outcompete low dominance males and thus will have greater access to females. However, during a peak in population density, offspring of low dominance males will outcompete high dominance male offspring, and the low dominance strategy would become more common in the population. As environmental conditions improve, high dominance male offspring will once again outcompete low dominance offspring. Therefore, the two strategies could be maintained in the population through fluctuating selection (e.g., Roff, 1997). Furthermore, during both of these periods, the opposite male strategy would be rare and would have a rare strategy advantage (Kokko *et al.*, 2007). The reproductive effort of bank voles is indeed negatively frequency-dependent in semi-natural field enclosure experiments (Mappes *et al.*, 2008b), thus providing an interesting example of the indirect genetic effect of an individual's neighbors on bank vole population dynamics and life history evolution. Each dominance strategy would be common during different phases of the cycle, during which the genetic covariance between signal and preference would be maintained. It has recently been hypothesized that only a small probability of signal reliability may be enough to maintain female preference for specific male characters (Narraway *et al.*, 2010). Whether once every 3–4 years is great enough to maintain such female preference, remains to be tested, but is an exciting possibility.

10.4.3 GEI on female reproductive success and sexual conflict

Sexually antagonistic effects have been found in the bank vole (Figure 10.2a,b) (Mills *et al.*, 2012; Mokkonen *et al.*, 2011) and this intralocus sexual conflict may have interesting consequences for the disruption of GEI-signal-preference genetic covariance. In our example of the GEI in bank voles, the dominance genes are sensitive to poor environmental conditions. If the environment is poor, selection against these genes will decrease T levels and reduce dominance in sons. The T levels of daughters may also be reduced, and their fecundity restored, should these genes have similar effects on them in poor environments. The GEI study also highlighted a negative relationship between the reproductive successes of full siblings when they had been reared in poor environments (Figure 10.3d) (Mills *et al.*, 2007a). Under poor rearing environments male offspring from dominant fathers had low mating success, therefore according to intralocus sexual conflict their female siblings would have high reproductive success and vice versa for offspring of subordinate fathers. Does a GEI therefore also exist for female reproductive success? This data suggests that there is considerable potential, and weak evidence (Mills *et al.*, 2007a) that GEI for female reproductive success is also present. Therefore, when male signal reliability is lost, that is, females gain no indirect fitness benefits from sons, indirect benefits may be recovered via daughter fitness. Some of these daughters would still be predicted to carry the same preference gene(s) that their mother carried, and if good environmental conditions were restored, such as during the crash phase of the density cycle, then male signal viability and thus reliability, would be manifest again in grandsons or great-grandsons. The focal mother would receive indirect genetic benefits after all, via daughter fitness (due to intralocus sexual conflict) as well as grandson/great-grandson fitness. More importantly, the GEI-signal-preference genetic covariance would be maintained.

We also found evidence for cryptic sex ratio bias in bank voles, as litters of high-quality females were biased towards daughters and low-quality females towards sons (Mills *et al.*, 2012). When sire genotypes have differential effects on sons versus daughters, female side blotched lizards, *Uta stansburiana*, and Gouldian finches, *Erythrura gouldiae*, are capable of altering progeny sex ratio accordingly (Calsbeek & Bonneaud, 2008; Calsbeek and Sinervo, 2004, Cox & Calsbeek, 2010; Katsuki *et al.*, 2012; Pryke & Griffith, 2009). It appears that female bank voles also use this strategy (Mills *et al.*, 2012). This result raises the possibility that whilst females cannot fully control sexual selection due to the important role played by male–male competition, females could still actively bias their litter sex ratio to increase their fitness either through daughters or sons as a function of current and future environmental conditions.

10.5 Summary

Bank vole population densities fluctuate with distinct density cycles in northern Fennoscandia (Korpela *et al.*, 2013) creating a variable selective environment, and a GEI has been found on male bank vole dominance (Mills *et al.*, 2007a). Therefore, under changing environmental conditions, the correlation between father and offspring fitness may vary. The change in offspring fitnesses may be explained by selection on different immune-related traits that differ between peak and crash years (Huitu *et al.*, 2007). The GEI for male fitness results in a disruption of the genetic covariance between the signal of male quality and the female's preference for it. But, environmental variation is also likely to play an important role in how this species responds to the breaking up of this covariance. We discuss three possible mechanisms that may maintain the genetic covariance between signal and preference. Firstly, the current literature suggests that it is unlikely that the reaction norms of female preferences will match those for male signals across environments. In bank voles, plastic female preferences will never fully compensate for the GEI of male dominance due to the significant role played by intra-sexual selection in male mating success. Secondly, bank voles show a phenotypic and genetic trade-off between immune response and T (Mills *et al.*, 2009; 2010; Schroderus *et al.*, 2010) and alternative male reproductive strategies in different environments may exist that are likely driven by differing risks of disease and density. If female mate preferences varied such that each alternative male strategy had evolved alongside a female preference for it, then genetic covariance would be maintained. Finally, the unreliability of male signals might be mitigated by the indirect genetic benefits of daughters via intralocus sexual conflict (Mills *et al.*, 2012), coupled with the presence of a GEI for female reproductive success (Mills *et al.*, 2007a). The bank vole provides a unique system in which evolutionary processes, such as GEI, can be studied.

References

Alatalo, R.V., Höglund, J., & Lundberg, A. (1991) Lekking in the black grouse – a test of male viability. *Nature,* 352: 155–156.

Alpert, P. & Simms, E.L. (2002) The relative advantages of plasticity and fixity in different environments: when is it good for a plant to adjust? *Evolutionary Ecology,* 16: 285–297.

Bakker, T.C.M. & Pomiankowski, A. (1995) The genetic basis of female mate preferences. *Journal of Evolutionary Biology,* 8: 129–171.

Beckerman, A.P., Benton, T.G., Ranta, E., Kaitala, V., & Lundberg, P. (2002) Population dynamic consequences of delayed life-history effects. *Trends in Ecology & Evolution,* 17: 263–269.

Bonduriansky, R. & Chenoweth, S.F. (2009) Intralocus sexual conflict. *Trends in Ecology & Evolution,* 24, 280–288.

Bonduriansky, R. & Rowe, L. (2005) Sexual selection, genetic architecture, and the condition dependence of body shape in the sexually dimorphic fly *Prochyliza xanthostoma* (Piophilidae). *Evolution,* 59: 138–151.

Brinck, A. & Hoffmeyer, I. (1974) Marking urine and preputial gland secretion of male bank voles (*Clethrionomys glareolus* L.). *Journal of Chemical Ecology,* 10: 1295–1307.

Brown, J. & Williams, J.D. (1972) The rodent preputial gland. *Mammal Review,* 2: 105–147.

Bujalska, G. (1985) Regulation of female maturation in *Clethrionomys* species, with special reference to an island population of *Clethrionomys glareolus*. *Annales Zoologici Fennici,* 22: 331–342.

Bussiere, L.F., Hunt, J., Stolting, K.N., Jennions, M.D., & Brooks, R. (2008) Mate choice for genetic quality when environments vary: suggestions for empirical progress. *Genetica,* 134: 69–78.

Calsbeek, R. & Bonneaud, C. (2008) Postcopulatory fertilization bias as a form of cryptic sexual selection. *Evolution,* 62: 1137–1148.

Calsbeek, R. & Sinervo, B. (2004) Within-clutch variation in offspring sex determined by differences in sire body size: cryptic mate choice in the wild. *Journal of Evolutionary Biology,* 17: 464–470.

Chaine, A.S. & Lyon, B.E. (2008) Adaptive plasticity in female mate choice dampens sexual selection on male ornaments in the lark bunting. *Science,* 319: 459–462.

Chippindale, A.K., Gibson, J.R., & Rice, W.R. (2001) Negative genetic correlation for adult fitness between sexes reveals ontogenetic conflict in *Drosophila*. *Proceedings of the National Academy of Sciences,* 98: 1671–1675.

Chitty, D. (1967) The natural selection of self-regulatory behavior in animal populations. *Proceedings of the Ecological Society of Australia,* 2: 51–78.

Comendant, T., Sinervo, B., Svensson, E., & Wingfield, J. (2003) Social competition, corticosterone and survival in female lizard morphs. *Journal of Evolutionary Biology,* 16: 948–955.

Cox, R.M. & Calsbeek, R. (2010) Cryptic sex-ratio bias provides indirect genetic benefits despite sexual conflict. *Science,* 328: 92–94.

Danielson-Francois, A.M., Kelly, J.K., & Greenfield, M.D. (2006) Genotype x environment interaction for male attractiveness in an acoustic moth: evidence for plasticity and canalization. *Journal of Evolutionary Biology,* 19: 532–542.

Danielson-Francois, A.M., Zhou, Y.H., & Greenfield, M.D. (2009) Indirect genetic effects and the lek paradox: inter-genotypic competition may strengthen genotype x environment interactions and conserve genetic variance. *Genetica,* 136: 27–36.

Eccard, J.A. & Ylonen, H. (2001) Initiation of breeding after winter in bank voles: effects of food and population density. *Canadian Journal of Zoology-Revue Canadienne De Zoologie,* 79: 1743–1753.

Elton, C.S. (1924) Periodic fluctuations in the numbers of animals: their causes and effects. *British Journal of Experimental Biology,* 2: 119–163.

Ergon, T., Lambin, X., & Stenseth, N.C. (2001a) Life-history traits of voles in a fluctuating population respond to the immediate environment. *Nature,* 411: 1043–1045.

Ergon, T., Mackinnon, J.L., Stenseth, N.C., Boonstra, R., & Lambin, X. (2001b) Mechanisms for delayed density-dependent reproductive traits in field voles, *Microtus agrestis*: the importance of inherited environmental effects. *Oikos,* 95: 185–197.

Fischer, H.S., Swaisgood, R.R., & Fitch-Snyder, H. (2003) Countermarking by male pygmy lorises (*Nycticebus pygmaeus*): do females use odor cues to select mates with high competitive ability? *Behavioral Ecology and Sociobiology,* 53: 123–130.

Fisher, R.A. (1930) *The Genetical Theory of Natural Selection,* Oxford, Oxford University Press.

Fry, J.D. (1996) The evolution of host specialization: Are trade-offs overrated? *American Naturalist,* 148: S84–S107.

Gillespie, J.H. & Turelli, M. (1989) Genotype-environment interactions and the maintenance of polygenic variation. *Genetics,* 121: 129–138.

Gosling, L.M. & Roberts, S.C. (2001) Scent-marking by mammals: cheat-proof signals to competitors and mates. *Advances in Studies of Behaviour,* 30: 169–217.

Greenfield, M.D., Danka, R.G., Gleason, J.M., Harris, B.R., & Zhou, Y. (2012) Genotype x environment interaction, environmental heterogeneity and the lek paradox. *Journal of Evolutionary Biology,* 25: 601–613.

Greenfield, M.D. & Rodriguez, R. (2004) Genotype-environment interaction and the reliability of mating signals. *Animal Behaviour,* 68: 1461–1468.

Greives, T.J., Mcglothlin, J.W., Jawor, J.M., Demas, G.E., & Ketterson, E.D. (2006) Testosterone and innate immune function inversely covary in a wild population of breeding Dark-Eyed Juncos (*Junco hyemalis*). *Functional Ecology,* 20: 812–818.

Gustafsson, L., Qvarnström, A., & Sheldon, B.C. (1995) Trade-offs between life-history traits and a secondary sexual character in male collared flycatchers. *Nature,* 375: 311–313.

Hairston, N.G. & Munns, W.R. (1984) The timing of copepod diapause as an evolutionary stable strategy. *American Naturalist,* 123: 733–751.

Hakkarainen, H., Koskela, E., Mappes, T., Soveri, T., Huhta, E., & Suorsa, P. (2007) Eimeria-parasites are associated with life history traits in island and mainland populations of the bank vole. *Parasitology,* 134: 23–31.

Hansson, L. (1985) *Clethrionomys* food – generic, specific and regional characteristics. *Annales Zoologici Fennici,* 22: 315–318.

Hasselquist, D., Marsh, J.A., Sherman, P.W., & Wingfield, J.C. (1999) Is avian humoral immunocompetence suppressed by testosterone? *Behavioral Ecology and Sociobiology,* 45: 167–175.

Haukisalmi, V. & Henttonen, H. (2000) Variability of helminth assemblages and populations in the bank vole *Clethrionomys glareolus*. *Polish Journal of Ecology,* 48: 219–231.

Hoffmann, A. (1991) Heritable variation for territorial success in field-collected *Drosophila melanogaster*. *American Naturalist,* 138: 668–679.

Hoffmeyer, I. (1982) Responses of female bank voles (*Clethrionomys glareolus*) to dominant vs subordinant conspecific males and to urine odours from dominant vs subordinant males. *Behavioral Neural Biology,* 36: 178–188.

Horne, T.J. & Ylönen, H. (1996) Female bank voles (*Clethrionomys glareolus*) prefer dominant males; but what if there is no choice? *Behavioral Ecology and Sociobiology,* 38: 401–405.

Horne, T.J. & Ylönen, H. (1998) Heritabilities of dominance-related traits in male bank voles *Clethrionomys glareolus*. *Evolution,* 41: 894–899.

Houde, A.E. (1992) Sex-linked heritability of a sexually selected character in a natural population of *Poecilia reticulata* (Pisces: Poceilidae) (guppies). *Heredity,* 69: 229–235.

Huitu, O., Jokinen, I., Korpimaki, E., Koskela, E., & Mappes, T. (2007) Phase dependence in winter physiological condition of cyclic voles. *Oikos,* 116: 565–577.

Huitu, O., Koivula, M., Korpimaki, E., Klemola, T., & Norrdahl, K. (2003) Winter food supply limits growth of northern vole populations in the absence of predation. *Ecology,* 84: 2108–2118.

Ingleby, F.C., Hunt, J., & Hosken, D.J. (2010) The role of genotype-by-environment interactions in sexual selection. *Journal of Evolutionary Biology,* 23: 2031–2045.

Innes, D.G.L. & Millar, J.S. (1994) Life-histories of *Clethrionomys* and *Microtus* (Microtinae). *Mammal Review,* 24: 179–207.

Jennions, M.D., Moller, A.P., & Petrie, M. (2001) Sexually selected traits and adult survival: A meta-analysis. *Quarterly Review of Biology,* 76: 3–36.

Jennions, M.D. & Petrie, M. (1997) Variation in mate choice and mating preferences: a review of cause and consequences. *Biological Review,* 72: 283–327.

Jia, F.-Y., Greenfield, M.D., & Collins, R.D. (2000) Genetic variance of sexually selected traits in waxmoths: Maintenance by genotype x environment interaction. *Evolution,* 54: 953–967.

Jonsson, P., Hartikainen, T., Koskela, E., & Mappes, T. (2002) Determinants of reproductive success in voles: space use in relation to food and litter size manipulation. *Evolutionary Ecology,* 16: 455–467.

Kallio, E.R., Begon, M., Henttonen, H., Koskela, E., Mappes, T., Vaheri, A., & Vapalahti, O. (2009) Cyclic hantavirus epidemics in humans predicted by rodent host dynamics. *Epidemics,* 1: 101–107.

Kaitala, V., Mappes, T., & Ylönen, H. (1997) Delayed female reproduction in equilibrium and chaotic populations. *Evolutionary Ecology,* 11: 105–126.

Kallio, E.R., Voutilainen, L., Vapalahti, O., Vaherl, A., Henttonen, H., Koskela, E., & Mappes, T. (2007) Endemic hantavirus infection impairs the winter survival of its rodent host. *Ecology,* 88: 1911–1916.

Katsuki, M., Harano, T., Miyatake, T., Okada, K., & Hosken, D.J. (2012) Intralocus sexual conflict and offspring sex ratio. *Ecology Letters,* 15: 193–197.

Klemme, I., Eccard, J.A., Gerlach, G., Horne, T.J., & Ylonen, H. (2006a) Does it pay to be a dominant male in a promiscuous species? *Annales Zoologici Fennici,* 43: 248–257.

Klemme, I., Eccard, J.A., & Ylonen, H. (2006b) Do female bank voles (Clethrionomys glareolus) mate multiply to improve on previous mates? *Behavioral Ecology and Sociobiology,* 60: 415–421.

Klemme, I. & Firman, R.C. (2013) Male house mice that have evolved with sperm competition have increased mating duration and paternity success. *Animal Behaviour,* 85: 751–758.

Klemme, I., Katajaho, S., Eccard, J.A., & Ylonen, H. (2012) Variable mode of estrus affects female decision for multiple mating. *Behavioral Ecology,* 23: 361–367.

Klemme, I., Ylonen, H., & Eccard, J.A. (2008) Long-term fitness benefits of polyandry in a small mammal, the bank vole Clethrionomys glareolus. *Proceedings of the Royal Society B-Biological Sciences,* 275: 1095–1100.

Koivula, M., Koskela, E., Mappes, T., & Oksanen, T.A. (2003) Cost of reproduction in the wild: Manipulation of reproductive effort in the bank vole. *Ecology,* 84: 398–405.

Kokko, H., Brooks, R., Jennions, M.D., & Morley, J. (2003) The evolution of mate choice and mating biases. *Proceedings of the Royal Society of London B,* 270: 653–664.

Kokko, H. & Heubel, K. (2008) Condition-dependence, genotype-by-environment interactions and the lek paradox. *Genetica,* 134: 55–62.

Kokko, H., Jennions, M.D., & Houde, A.E. (2007) Evolution of frequency-dependent mate choice: keeping up with fashion trends. *Proceedings of the Royal Society of London B,* 274: 1317–1324.

Korpela, K., Delgado, M., Henttonen, H., Korpimäki, E., Koskela, E., Ovaskainen, O., et al. (2013) Nonlinear effects of climate on boreal rodent dynamics: mild winters do not negate high-amplitude cycles. *Global Change Biology,* 19: 697–710.

Koskela, E., Jonsson, P., Hartikainen, T., & Mappes, T. (1998) Limitation of reproductive success by food availability and litter size in the bank vole, *Clethrionomys glareolus*. *Proceedings of the Royal Society of London B,* 265: 1129–1134.

Koskela, E., Mappes, T., & Ylönen, H. (1999) Experimental manipulation of breeding density and litter size: effects on reproductive success in the bank vole. *Journal of Animal Ecology,* 68: 513–521.

Koskela, E., Mappes, T., Niskanen, T., & Rutkowska, J. (2009) Maternal investment in relation to sex ratio and offspring number in a small mammal – a case for Trivers and Willard theory? *Journal of Animal Ecology,* 78: 1007–1014.

Krebs, C.J. & Myers, J.H. (1974) Population cycles in small mammals. In *Advances in Ecological Research* (MacFadyen, A. ed.). London, Academic Press Inc.

Kruczek, M. (1997) Male rank and female choice in the bank vole, *Clethrionomys glareolus*. *Behavioural Processes,* 40: 171–176.

Kruczek, M. & Marchlewska-Koj, A. (1986) Puberty delay of bank voles females in a high-density population. *Biology of Reproduction,* 35: 537–541.

Kruczek, M. (1994) Responses of female bank voles *Clethrionomys glareolus* to male chemosignals. *Acta Theriologica,* 39: 249–255.

Lande, R. (1980) Sexual dimorphism, sexual selection, and adaptation in polygenic characters *Evolution,* 34: 292–305.

Lesna, I. & Sabelis, M.W. (1999) Diet-dependent female choice for males with "good genes" in a soil predatory mite. *Nature,* 401: 581–584.

Levins, R. (1968) *Evolution in Changing Environments,* Princeton, NJ, Princeton University Press.

Lindström, J. (1999) Early development and fitness in birds and mammals. *Trends in Ecology & Evolution,* 14: 343–348.

Lively, C.M. (1986) Canalization versus developmental conversion in a spatially-variable environment. *American Naturalist,* 128: 561–572.

Lochmiller, R.L., Vestey, M.R. & Boren, J.C. (1993) Relationship between protein nutritional status and immunocompetence in Northern Bobwhite chicks. *Auk,* 110: 503–510.

Luster, M.I., Portier, C., Pait, D.G., Rosenthal, G.J., Germolec, D.R., Corsini, E., et al. (1993) Risk assessment in immunotoxicology. II. Relationships between immune and host resistance tests. *Fundamental and Applied Toxicology,* 21: 71–82.

Lynch, K.S., Rand, A.S., Ryan, M.J., & Wilczynski, W. (2005) Plasticity in female mate choice associated with changing reproductive states. *Animal Behaviour,* 69: 689–699.

MacDonald, D. (2001) *The Encylopedia of Mammals,* Oxford, Andromeda Oxford Limited.

Mank, J.E. (2007) The evolution of sexually selected traits and antagonistic androgen expression in actinopterygiian fishes. *American Naturalist,* 169: 142–149.

Mappes, T., Grapputo, A., Hakkarainen, H., Huhta, E., Koskela, E., Saunanen, R., & Suorsa, P. (2008a) Island selection on mammalian life-histories: genetic differentiation in offspring size. *BMC Evolutionary Biology,* 8: 296.

Mappes, T., Koivula, M., Koskela, E., Oksanen, T.A., Savolainen, T., & Sinervo, B. (2008b) Frequency and density-dependent selection on life-history strategies – a field experiment. *PLoS One,* 3: e1687.

Mappes, T. & Koskela, E. (2004) Genetic basis of the trade-off between offspring number and quality in the bank vole. *Evolution,* 58: 645–650.

Mappes, T., Koskela, E., & Ylönen, H. (1995a) Reproductive costs and litter size in the bank vole. *Proceedings of the Royal Society of London B,* 261: 19–24.

Mappes, T., Ylönen, H., & Viitala, J. (1995b) Higher reproductive success among kin groups of bank voles (*Clethrionomys glareolus*). *Ecology,* 76: 1276–1282.

Mappes, T., Aspi, J., Koskela, E., Mills, S.C., Poikonen, T., & Tuomi, J. (2012) Advantage of rare infanticide strategies in an invasion experiment of behavioural polymorphism. *Nature Communications,* 3: 611.

Mazurkiewicz, M. (1971) Shape, size and distribution of home ranges of *Clethrionomys glareolus* (Shreber, 1780). *Acta Theriologica,* 16: 23–60.

Mills, S.C., Alatalo, R.V., Koskela, E., Mappes, J., Mappes, T., & Oksanen, T.A. (2007a) Signal reliability compromised by genotype by environment interaction and potential mechanisms for its preservation. *Evolution,* 61–67: 1748–1757.

Mills, S.C., Grapputo, A., Jokinen, I., Koskela, E., Mappes, T., Oksanen, T.A., & Poikonen, T. (2009) Testosterone-mediated effects on fitness-related phenotypic traits and fitness. *American Naturalist,* 173: 475–487.

Mills, S.C., Grapputo, A., Jokinen, I., Koskela, E., Mappes, T., & Poikonen, T. (2010) Fitness trade-offs mediated by immunosuppression costs in a small mammal. *Evolution,* 64: 166–179.

Mills, S.C., Grapputo, A., Koskela, E., & Mappes, T. (2007b) Quantitative measure of sexual selection with respect to the operational sex ratio: a comparison of selection indices. *Proceedings of the Royal Society of London B,* 274: 143–150.

Mills, S.C., Koskela, E., & Mappes, T. (2012) Intralocus sexual conflict for fitness: sexually antagonistic alleles for testosterone. *Proceedings of the Royal Society B-Biological Sciences,* 279: 1889–1895.

Mokkonen, M., Kokko, H., Koskela, E., Lehtonen, J., Mappes, T., Martiskainen, H. & Mills, S.C. (2011) Negative frequency-dependent selection of sexually antagonistic alleles in *Myodes glareolus*. *Science,* 334: 972–974.

Mokkonen, M., Koskela, E., Mappes, T., & Mills, S.C. (2012) Sexual antagonism for testosterone maintains multiple mating behaviour. *Journal of Animal Ecology,* 81: 277–283.

Moller, A.P. & De Lope, F. (1995) Differential allocation and sexual ornamentation. *Evolution,* 49: 1290–1292.

Narraway, C., Hunt, J., Wedell, N., & Hosken, D.J. (2010) Genotype-by-environment interactions for female preference. *Journal of Evolutionary Biology,* 23: 2550–2557.

Norrdahl, K. & Korpimäki, E. (1995) Mortality factors in a cyclic vole population. *Proceedings of the Royal Society of London B,* 261: 49–53.

Norris, K. & Evans, M.R. (2000) Ecological immunology: life history trade-offs and immune defense in birds. *Behavioral Ecology,* 11: 19–26.

Oksanen, T.A., Alatalo, R.V., Horne, T.J., Koskela, E., Mappes, J., & Mappes, T. (1999) Maternal effort and male quality in the bank vole, *Clethrionomys glareolus*. *Proceedings of the Royal Society of London B,* 266: 1495–1499.

Oksanen, T.A., Jokinen, I., Koskela, E., Mappes, T., & Vilpas, H. (2003) Manipulation of offspring number and size: benefits of large body size at birth depend upon the rearing environment. *Journal of Animal Ecology,* 72: 321–330.

Oksanen, T.A., Koivula, M., Koskela, E., & Mappes, T. (2007) The cost of reproduction induced by body size at birth and breeding density. *Evolution,* 61: 2822–2831.

Ostfeld, R. (1985) Limiting resources and territoriality in microtine rodents. *American Naturalist,* 126: 1–15.

Ostfeld, R.S. & Canham, C.D. (1995) Density-dependent processes in meadow voles – an experimental approach. *Ecology,* 76: 521–532.

Prévot-Julliard, A.C., Henttonen, H., Yoccoz, N.G., & Stenseth, N.C. (1999) Delayed maturation in female bank voles: optimal decision or social constraint? *Journal of Animal Ecology,* 68: 684–697.

Pryke, S.R. & Griffith, S.C. (2009) Genetic incompatibility drives sex allocation and maternal investment in a polymorphic finch. *Science,* 323: 1605–1607.

Qvarnstrom, A., Brommer, J.E., & Gustafsson, L. (2006) Testing the genetics underlying the co-evolution of mate choice and ornament in the wild. *Nature,* 441: 84–86.

Qvarnstrom, A., Part, T., & Sheldon, B.C. (2000) Adaptive plasticity in mate preference linked to differences in reproductive effort. *Nature,* 405: 344–347.

Radwan, J., Chadzinska, M., Cichon, M., Mills, S.C., Matula, B., Sadowska, E.T., et al. (2006) Metabolic costs of sexual advertisement in the bank vole, *Clethrionomys glareolus*. *Evolutionary Ecology Research,* 8: 859–869.

Rice, W.R. (1984) Sex chromosomes and the evolution of sexual dimorphism. *Evolution,* 38: 735–742.

Rikalainen, K., Aspi, J., Galarza, J.A., Koskela, E., & Mappes, T. (2012) Maintenance of genetic diversity in cyclic populations – a longitudinal analysis in *Myodes glareolus*. *Ecology and Evolution,* 2: 1491–1502.

Robinson, M.R., Van Doorn, G.S., Gustafsson, L., & Qvarnstrom, A. (2012) Environment-dependent selection on mate choice in a natural population of birds. *Ecology Letters,* 15: 611–618.

Rodriguez, R.L. & Greenfield, M.D. (2003) Genetic variance and phenotypic plasticity in a component of female mate choice in an ultrasonic moth. *Evolution,* 57: 1304–1313.

Roff, D.A. (1997) *Evolutionary Quantitative Genetics,* New York, International Thomson Publishing.

Schlichting, C.D. & Pigliucci, M. (1998) *Phenotypic Evolution: A Reaction Norm Perspective,* Sunderland, MA, Sinauer Associates, Inc.

Schroderus, E., Jokinen, I., Koivula, M., Koskela, E., Mappes, T., Mills, S.C., et al. (2010) Intra- and intersexual trade-offs between testosterone and immune system: implications for sexual and sexually antagonistic selection. *American Naturalist,* 176: E90–E97.

Schroderus, E., Koivula, M., Koskela, E., Mappes, T., Oksanen, T.A., & Poikonen, T. (2012) Can number and size of offspring increase simultaneously? A central life-history trade-off reconsidered. *BMC Evolutionary Biology,* 12: 44.

Singh, J. & Handelsman, D.J. (1996) Neonatal administration of FSH increases Sertoli cell numbers and spermatogenesis in gonadotrophin-deficient (*hpg*) mice. *Journal of Endocrinology,* 151: 37–48.

Soveri, T., Henttonen, H., Rudback, E., Schildt, R., Tanskanen, R., Husu-Kallio, J., et al. (2000) Disease patterns in field and bank vole populations during a cyclic decline in central Finland. *Comparative Immunology Microbiology and Infectious Diseases,* 23: 73–89.

Spaliviero, J.A., Jimenez, M., Allan, C.M., & Handelsman, D.J. (2004) Luteinizing hormone receptor-mediator effects on initiation of spermatogenesis in gonadotrophin-deficient (*hpg*) mice are replicated by testosterone. *Biology of Reproduction,* 70: 32–38.

Sriraman, V., Sairam, M.R., & Jagannadha, R.A. (2004) Evaluation of relative role of LH and FSH in restoration of spermatogenesis using ethanedimethylsulphonate-treated adult rats. *Reproductive Biomedical Online,* 8: 167–174.

Stenseth, N.C. (1985) Geographic distribution of *Clethrionomys* species. *Annales Zoologici Fennici,* 22: 215–219.

Svensson, E., Raberg, L., Koch, C., & Hasselquist, D. (1998) Energetic stress, immunosuppression and the costs of an antibody response. *Functional Ecology,* 1: 912–919.

Svensson, E. & Skarstein, F. (1997) The meeting of two cultures: bridging the gap between ecology and immunology. *Trends in Ecology and Evolution,* 12: 92–93.

Tomkins, J.L., Radwan, J., Kotiaho, J.S., & Tregenza, T. (2004) Genic capture and resolving the lek paradox. *Trends in Ecology & Evolution,* 19: 323–328.

Tuomi, J., Agrell, J., & Mappes, T. (1997) On the evolutionary stability of female infanticide. *Behavioral Ecology and Sociobiology,* 40: 227–233.

Westneat, D.F. & Sih, A. (2009) Sexual conflict as a partitioning of selection. *Biology Letters,* 5: 675–677.
Zahavi, A. (1975) Mate selection – a selection for a handicap. *Journal of Theoretical Biology,* 67: 603–606.
Zahavi, A. (1977) The cost of honesty (further remarks on the handicap principle). *Journal of Theoretical Biology,* 67: 603–605.
Zhou, Y.H., Kuster, H.K., Pettis, J.S., Danka, R.G., Gleason, J.M., & Greenfield, M.D. (2008) Reaction norm variants for male calling song in populations of *Achroia grisella* (Lepidoptera : Pyralidae): Toward a resolution of the lek paradox. *Evolution,* 62: 1317–1334.
Zuk, M. & Stoehr, A.M. (2002) Immune defense and host life history. *American Naturalist,* 160: S9–S22.