

Complex community and evolutionary responses to habitat fragmentation and habitat edges: what can we learn from insect science?

Shannon M Murphy¹, Amy H Battocletti², Robin M Tinghitella¹,
Gina M Wimp² and Leslie Ries²



Habitat fragmentation is the primary factor leading to species extinction worldwide and understanding how species respond to habitat edges is critical for understanding the effects of fragmentation on insect diversity in both natural and managed landscapes. Most studies on insect responses to the habitat edge focus on bottom-up changes in resources. Only a few recent studies have examined multi-trophic responses to habitat edges; the results of these studies highlight the problem that we lack a conceptual framework to understand the complex results observed when a single species' response to an edge 'cascades' throughout the food web in ways that are currently not predictable. Recent research from insect systems suggests that habitat edge responses cascade both up and down multi-trophic foodwebs and these altered species interactions may affect evolutionary processes. Future studies that investigate the effects of habitat edges on both ecological and evolutionary dynamics can help to fill these knowledge gaps and we suggest that insects, with short generation times, present an ideal opportunity to do so.

Addresses

¹ Department of Biological Sciences, University of Denver, Denver, CO 80208, USA

² Biology Department, Georgetown University, Washington, D.C. 20057, USA

Corresponding author: Murphy, Shannon M
(Shannon.M.Murphy@du.edu)

Current Opinion in Insect Science 2016, 14:61–65

This review comes from a themed issue on **Ecology/Parasites/Parasitoids/Biological control**

Edited by **Sergio Rasmann** and **Kailen Mooney**

<http://dx.doi.org/10.1016/j.cois.2016.01.007>

2214-5745/© 2016 Elsevier Inc. All rights reserved.

Introduction

Habitat loss and fragmentation is widely considered to be the primary factor leading to species extinction worldwide. Although multiple mechanisms contribute to species losses in fragmented habitats, fragmentation is usually associated with increased edge habitat [1], and

most effects of fragmentation attributed to patch area are actually scaled-up edge effects [2]. Compared with core (interior) habitat, edge habitats are subject to different abiotic conditions, such as variation in solar radiation, temperature, wind, soil moisture and humidity [3^{**}]. The severity of the changes in abiotic conditions can depend on how 'soft' or 'hard' the contrast is between the two abutting habitats. Understanding how species respond to habitat edges is critical for understanding the effects of fragmentation on diversity in both natural and managed landscapes [3^{**}]. Yet, despite recent advances in understanding single species responses to habitat edges, we lack a framework to understand more complex interactions or evolutionary processes. Here, we synthesize the literature on ecological and evolutionary responses to edges with a focus on empirical examples from insect science; these well-studied systems provide a gateway to understand mechanisms, interactions and, where generation times are short, evolutionary changes in real time.

Ecological responses to habitat edges

Bottom-up drivers of insect responses to habitat edges

The factors underlying single-species edge responses have been formalized into an Edge Resource Model (ERM) that created a simple set of predictions for any species at any edge type based on resource quality and distribution in adjoining habitats [4]. The model was based on two fundamental mechanisms that are unique to edges: (1) ecological flows of species/energy/material from one adjoining habitat into another creating a gradient of habitat quality near the edge and (2) better access to spatially separated resources is maximized at edges (also known as 'cross-boundary subsidies'). The ERM has been a useful model for studying insect responses to habitat edges because many edge responses result from bottom-up changes in resources. The typical prediction is that microclimatic changes near edges impact plant distribution or quality, and variation in these key resources then cascades to alter herbivore and predator distributions. Notably, changes in the physical environment along the habitat edge can change habitat structure, which may increase the interception of allochthonous nutrients (e.g. through increased deposition [5]) and thereby increase plant quality for herbivores. For example, although density of a key host plant declined in patch edges during colonization after the Mt. St. Helen's eruption, higher nutritive quality was shown to lead to insect herbivore

outbreaks [6]. Such increases in plant quality along the habitat edge may explain why a recent meta-analysis found an overall increase in insect herbivore abundance, richness, and plant herbivory along habitat edges relative to core habitats [7]. The ERM provides a mechanistic explanation for many edge responses reported in the literature [3**], but it is limited to single species responses and does not incorporate multi-species interactions or predict how shifts in the community along a habitat edge alters species interactions or top-down effects.

Top-down drivers of insect responses to habitat edges

The consequences of fragmentation for top-down control of species have also been considered in the literature. A recent meta-analysis found increased consumption in edge habitats compared to interiors [8**]. Notably, this increased top-down effect was driven primarily by herbivores feeding on plants, and in particular by dietary generalists, not specialists. Further, this meta-analysis found no evidence that higher trophic level organisms such as predators or parasitoids increased consumption in edge habitats (but see [9**], discussed below in ‘multi-trophic interactions and community patterns’). Although herbivory rates change near edges, top-down mechanisms such as changes in predation rate have not been integrated into formal predictions of edge responses and the edge literature is conflicted about how predators respond to edges. Theory related more generally to habitat fragmentation, not just habitat edges, predicts that higher-trophic-level consumers should be particularly vulnerable to habitat fragmentation (e.g. [10]); the predicted negative impact of fragmentation on predators is based on Island Biogeographic Theory [11] and the idea that patch size and isolation have greater impacts at higher trophic levels [10,12]. Despite the fact that edge effects dominate in fragmented habitats, a common generalization has emerged from the edge literature that generalist predators increase along habitat edges [13]. The belief that predators respond positively to edges may persist because the edge effect literature is biased towards generalist predators of avian nests [14], which makes it difficult to ascertain whether this edge-predator effect is widely applicable to other taxa. Thus, the conflicting views of predators (that they often thrive at edges, but are especially vulnerable to fragmentation) may come from focusing on different predator communities and may be biased towards generalist, vertebrate mesopredators. In support of this assertion, studies of insects in agricultural systems have primarily demonstrated that predators track transitional gradients in prey resources across the edge (e.g. [15]), and positive edge responses are relatively rare. A better understanding of how top-down interactions disrupt species mapping onto critical resources is essential for predicting population and community responses to habitat edges.

Multi-trophic interactions and community patterns

Landscape and conservation ecologists have studied how habitat fragmentation affects individual species as well as

communities for decades [16] and recent studies have tried to understand how fragmentation affects food web dynamics [reviewed in 8**,17]. However, most examinations of species interactions in fragmented habitats are restricted to two-species models [8**] and the few studies that have examined how habitat fragmentation affects multi-trophic interactions focused on isolation and/or area effects (e.g. [18–20]), not the effects of habitat edges *per se* (but see [9**]). Only two studies have examined responses to habitat edges from a community perspective, and both found top-down effects on herbivores. For example, Evans *et al.* [21*] found decreased herbivore consumption near edges, a result of trophic interactions among ants, aphids, and a defoliating herbivore. In another multi-trophic study, Wimp *et al.* [9**] demonstrated that predicted declines of planthopper herbivores near edges were not explained by bottom-up effects on resources, which did not vary in quality or quantity between edge and core habitats, but instead were likely due to predator avoidance. Predators may also ‘spillover’ into natural fragments from managed habitat at higher rates than other trophic levels [22*] and bias in dispersal patterns may concentrate parasitoids at edges [23] thereby increasing top-down control along edges. These results suggest that top-down selective pressures can drive species responses to habitat edges and argue for incorporating predator/parasitoid densities as an additional resource that may drive herbivore edge responses.

Most studies that examined the impact of habitat edges on insect communities have quantified changes in abundance or species richness, but did not examine changes in community structure, critical resources or trophic interactions that may have led to those responses [17]. These studies have largely examined the prediction that insect diversity and abundance will be greater along habitat edges relative to the interior because edges represent the convergence of two distinct habitats. While some studies have found higher arthropod diversity in edge relative to interior habitats, others have found no response, or the reverse, often with inconsistent results among different taxa in the same study [24–27,28*]. It may therefore be useful to consider how feeding specialization and functional group might influence insect community responses to the habitat edge. Previous studies have found that specialist herbivores are more likely to be negatively impacted by the habitat edge relative to generalist herbivores [7]. For example, specialist planthoppers are negatively affected by edges due to the absence of food in the adjacent habitat [9**,29], and this negative response intensifies when there is a high degree of environmental dissimilarity (or contrast) between the two adjoining habitats [24,29]. However, because these specialist herbivores are unwilling to cross from suitable to unsuitable habitat, they are often found in aggregations near the edge, and this can lead to increased rates of parasitism, despite declines in parasitoid abundance along

the edge [29,30]. Thus, edges may increase resource variability, with consequences for multiple trophic levels, and specialists may be especially sensitive to such variation.

Evolutionary consequences of altered ecological interactions

Changes in the distribution of critical resources and top-down pressures in a fragmented landscape alter species abundance, which may in turn have evolutionary consequences. The dominant evolutionary force affecting organisms living within anthropogenically fragmented habitats may be genetic drift (e.g. [31]), which acts to reduce variation in small, isolated populations. Gene flow can alleviate the effects of drift and enable the maintenance of variation in well-connected habitats [31,32]. Adaptations and phenotypic plasticity, particularly in dispersal morphology, may also facilitate gene flow [33].

Our understanding of evolutionary processes in fragmented habitats comes mainly from studies of isolated populations, but changes in population dynamics in edge habitats may also have evolutionary consequences despite not being isolated from patch interiors [28*]. Altered top-down forces in edge habitats may primarily influence insect evolution via selective pressures associated with predation and reduced densities. Altered bottom-up forces may occur via changes in plant intraspecific variation, which can then influence arthropod density, composition, intraspecific variation and even sexual phenotypes and assortative mating [34–36]. Plants' genotypic variation can be altered at edges by unique reproductive dynamics. For instance, plants may exhibit high homozygosity in edge habitats due to increased selfing rates in response to both pollen and pollinator limitation [31,37]. Relative to outbred individuals, inbreeding may induce physiological changes that negatively affect survival and reproduction, and thus impact herbivores via reduced resource quality. Inbreeding may also reduce tolerance to herbivores, potentially exacerbating demographic declines in low-density populations [38]. Alternately, edges have been proposed to be hotspots of plant genetic variation due to increased habitat heterogeneity and distance-limited dispersal [39] and this has been shown to be true at ecotones between biomes [3**].

Plants can also mediate indirect effects among arthropods and influence eco-evolutionary dynamics [40]. For example, changes in plant genotype resulting from directional selection imposed by a single herbivore species may impact resistance to other herbivore species [41], and priority effects of different early season herbivores can alter plant responses to herbivory and thereby affect community arthropod composition (e.g. [42]). Changes in plant genotypic variation in edge habitats compared to core habitats may have important implications for insects, but whether these effects are strong enough to alter

evolutionary trajectories between edges and interiors is currently unknown.

It is also possible that effects of habitat fragmentation on demography, resource availability, connectivity, and interspecific interactions could alter social interactions within and between the sexes. Yet, our understanding of how habitat edges and fragmentation affect sexual selection is limited [43**,44] and comes largely from vertebrate systems [44], but insects with short generation times present an ideal opportunity to study these questions (see [45] for a comprehensive treatment of global change on sexual selection). Because sexual selection decreases effective population size and can drive rapid and divergent evolution of sexually selected traits, leading to speciation [46,47], it may be tied closely to the persistence of edge populations. Sexual selection is largely driven by the availability of mates, which habitat fragmentation alters in two primary ways: reduced population size or density and biased sex ratios within fragments (because of demographic stochasticity or sex-biased dispersal, e.g. [48–50]). In the simplest case, theory predicts that the proportion of males unsuccessful in competition and female choice is highest at high male density [51] and male competition is most intense at male-biased operational sex ratios (but see [52,53]). Further, females can afford to be more selective when males are readily available [54]. Thus, in fragmented habitats with reduced mate availability and connectivity, we might expect relaxed sexual selection to facilitate population persistence, similar to island systems [55].

Encounter rates with competitors and natural enemies also alter the nature and strength of sexual selection [56,57], and as discussed above, interactions among these species are likely altered in edge habitats. There is a rich literature on evolutionary and plastic responses of sexually selected characters to natural enemies, including decreased conspicuousness of sexual signals and behaviour, and relaxed female mating decisions under high predation or parasitization [56,58]. Moreover, the link between habitat fragmentation and rapid divergence of sexual traits was recently made in *Gambusia* fish in Bahamian streams; genital shape and allometry repeatedly diverged in fragmented locations [43**] due to decreased predator density *and* increased conspecific density. Similarly, altered parasitism in insect systems could drive rapid evolution of signals that confer reproductive isolation (e.g. [59]) in edge habitats. However, how altered species interactions in edge habitats influences sexual selection has not yet been investigated in insects.

Conclusions and perspectives

Studying species responses to habitat edges without a community perspective is problematic because it is difficult to make sense of complex, variable community responses. Yet one of the fundamental assumptions

within the edge literature is that a single species' response to an edge may 'cascade' throughout the community and has the potential to impact all species connected throughout a web of interactions. We suggest that habitat edge responses may cascade both up and down multi-trophic foodwebs and these altered species interactions likely affect evolutionary processes, but these have so far not been well studied. An expansion of edge theory to improve its predictive power for community responses is needed. Studies investigating the effects of edges on linked trophic dynamics and foodwebs may help to fill these knowledge gaps if they can elucidate the underlying mechanisms that cause edge responses, and we suggest that insects with short generation times present an ideal opportunity to do so.

Acknowledgements

We are grateful to Sergio Rasmann and Kailen Mooney for their invitation to write this piece. We thank the University of Denver Organismal Biologists, two anonymous reviewers and Kailen Mooney for helpful comments that greatly improved our manuscript.

References and recommended reading

Papers of particular interest, published within the period of review, have been highlighted as:

- of special interest
 - of outstanding interest
1. Sisk TD, Haddad NM, Ehrlich PR: **Bird assemblages in patchy woodlands: modeling the effects of edge and matrix habitats.** *Ecol Appl* 1997, **7**:1170-1180.
 2. Fletcher RJ, Ries L, Battin J, Chalfoun AD: **The role of habitat area and edge in fragmented landscapes: definitively distinct or inevitably intertwined?** *Can J Zool* 2007, **85**:1017-1030.
 3. Ries L, Fletcher RJ, Battin J, Sisk TD: **Ecological responses to habitat edges: mechanisms, models, and variability explained.** *Ann Rev Ecol Syst* 2004, **35**:491-522.
- This review presents the first model that can be used to make *a priori* predictions of edge responses for any species in any landscape. The review further tests the model on four different taxa (birds, mammals, plants, butterflies) and presents mechanisms that underlie the considerable variation of responses that are reported in the literature.
4. Ries L, Sisk TD: **A predictive model of edge effects.** *Ecology* 2004, **85**:2917-2926.
 5. Devaemincq R, De Schrijver A, Hermy M: **Variation in throughfall deposition across a deciduous beech (*Fagus sylvatica* L.) forest edge in Flanders.** *Sci Total Environ* 2005, **337**:241-252.
 6. Fagan WE, Bishop JG, Schade JD: **Spatially structured herbivory and primary succession at Mount St. Helens: field surveys and experimental growth studies suggest a role for nutrients.** *Ecol Entomol* 2004, **29**:398-409.
 7. De Carvalho Guimaraes CD, Viana JPR, Cornelissen T: **A meta-analysis of the effects of fragmentation on herbivorous insects.** *Environ Entomol* 2014, **43**:537-545.
 8. Martinson HM, Fagan WF: **Trophic disruption: a meta-analysis of how habitat fragmentation affects resource consumption in terrestrial arthropod systems.** *Ecol Lett* 2014, **17**:1178-1189.
- This paper demonstrates that most examinations of species interactions in fragmented habitats and along edges are restricted to two-species models.
9. Wimp GM, Murphy SM, Lewis D, Ries L: **Do edge responses cascade up or down a multi-trophic foodweb?** *Ecol Lett* 2011, **14**:863-870.
- The first empirical study of whether and how edge effects cascade throughout a complex, multi-tier food web. The study found that predicted declines of herbivores near edges were not explained by their

resources, but instead were likely due to predator avoidance. This study highlights the importance of studying edge responses from a community perspective.

10. Holt RD, Lawton JH, Polis GA, Martinez ND: **Trophic rank and the species-area relationship.** *Ecology* 1999, **80**:1495-1504.
 11. MacArthur RH, Wilson EO: *The Theory of Island Biogeography.* Princeton University Press; 1967.
 12. Ewers RM, Didham RK: **Confounding factors in the detection of species responses to habitat fragmentation.** *Biol Rev* 2006, **81**:117-142.
 13. Lahti DC: **The "edge effect on nest predation" hypothesis after twenty years.** *Biol Conserv* 2001, **99**:365-374.
 14. Chalfoun AD, Thompson FR, Ratnaswamy MJ: **Nest predators and fragmentation: a review and meta-analysis.** *Conserv Biol* 2002, **16**:306-318.
 15. Rand TA, Tyljanakis JM, Tschamtké T: **Spillover edge effects: the dispersal of agriculturally subsidized insect natural enemies into adjacent natural habitats.** *Ecol Lett* 2006, **9**:603-614.
 16. Saunders DA, Hobbs RJ, Margules CR: **Biological consequences of ecosystem fragmentation: a review.** *Conserv Biol* 1991, **5**:18-32.
 17. Tschamtké T, Brandl R: **Plant-insect interactions in fragmented landscapes.** *Ann Rev Entomol* 2004, **49**:405-430.
 18. Cagnolo L, Valladares G, Salvo A, Cabido M, Zak M: **Habitat fragmentation and species loss across three interacting trophic levels: effects of life-history and food-web traits.** *Conserv Biol* 2009, **23**:1167-1175.
 19. Cronin JT: **Host-parasitoid extinction and colonization in a fragmented prairie landscape.** *Oecologia* 2004, **139**:503-514.
 20. Komonen A, Penttilä R, Lindgren M, Hanski I: **Forest fragmentation truncates a food chain based on an old-growth forest bracket fungus.** *Oikos* 2000, **90**:119-126.
 21. Evans DM, Turley NE, Tewksbury JJ: **Habitat edge effects alter ant-guard protection against herbivory.** *Landscape Ecol* 2013, **28**:1743-1754.
- This paper is one of the few to study edge effects from a multi-species perspective.
22. Frost CM, Didham RK, Rand TA, Peralta G, Tyljanakis JM: **Community-level net spillover of natural enemies from managed to natural forest.** *Ecology* 2015, **96**:193-202.
- This is the first study to experimentally show a net cross-edge spillover of predators from a managed habitat into a natural habitat fragment.
23. Reeve JD, Cronin JT: **Edge behavior in a minute parasitic wasp.** *J Anim Ecol* 2010, **79**:483-490.
 24. Peyras M, Vespa NI, Bellocq MI, Zurita G: **Quantifying edge effects: the role of habitat contrast and species specialization.** *J Insect Conserv* 2013, **17**:807-820.
 25. Rossetti MR, Salvo A, Videla M, Valladares G: **Forest remnants contribute to parasitoid conservation: experimental evaluation of parasitism on a leafminer host.** *J Insect Conserv* 2013, **17**:1137-1144.
 26. Rotholz E, Mandelik Y: **Roadside habitats: effects on diversity and composition of plant, arthropod, and small mammal communities.** *Biodivers Conserv* 2013, **22**:1017-1031.
 27. Gonzalez E, Salvo A, Valladares G: **Arthropods on plants in a fragmented Neotropical dry forest: a functional analysis of area loss and edge effects.** *Insect Sci* 2015, **22**:129-138.
 28. Peralta G, Frost CM, Didham RK, Varsani A, Tyljanakis JM: **Phylogenetic diversity and co-evolutionary signals among trophic levels change across a habitat edge.** *J Anim Ecol* 2015, **84**:364-372.
- This study found that phylogenetic diversity varied significantly across a habitat edge between managed and natural forests and that co-evolutionary signals differed across trophic levels.
29. Cronin JT: **Habitat edges, within-patch dispersion of hosts, and parasitoid oviposition behavior.** *Ecology* 2009, **90**:196-207.

30. Valladares G, Salvo A, Cagnolo L: **Habitat fragmentation effects on trophic processes of insect-plant food webs.** *Conserv Biol* 2006, **20**:212-217.
31. Aguilar R, Quesada M, Ashworth L, Herreras-Diego Y, Lobo J: **Genetic consequences of habitat fragmentation in plant populations: susceptible signals in plant traits and methodological approaches.** *Mol Ecol* 2008, **17**:5177-5188.
32. Matesanz S, Gomez-Fernandez A, Alcocer I, Escudero A: **Fragment size does not matter when you are well connected: effects of fragmentation on fitness of coexisting gypsophiles.** *Plant Biol* 2015, **17**:1047-1056.
33. Kanuch P, Jarcuska B, Schlosserova D, Sliacka A, Paule L, Kristin A: **Landscape configuration determines gene flow and phenotype in a flightless forest-edge ground-dwelling bush-cricket, *Pholidoptera griseoptera*.** *Evol Ecol* 2012, **26**:1331-1343.
34. Rebar D, Rodriguez RL: **Insect mating signal and mate preference phenotypes covary among host plant genotypes.** *Evolution* 2015, **69**:602-610.
35. Wimp GM, Young WP, Woolbright SA, Martinsen GD, Keim P, Whitham TG: **Conserving plant genetic diversity for dependent animal communities.** *Ecol Lett* 2004, **7**:776-780.
36. Lamit LJ, Busby PE, Lau MK, Compson ZG, Wojtowicz T, Keith AR, Zinkgraf MS, Schweitzer JA, Shuster SM, Gehring CA et al.: **Tree genotype mediates covariance among communities from microbes to lichens and arthropods.** *J Ecol* 2015, **103**:840-850.
37. Eckert CG, Kalisz S, Geber MA, Sargent R, Elle E, Cheptou P-O, Goodwillie C, Johnston MO, Kelly JK, Moeller DA et al.: **Plant mating systems in a changing world.** *Trends Ecol Evol* 2010, **25**:35-43.
38. Shaw RG, Wagenius S, Geyer CJ: **The susceptibility of *Echinacea angustifolia* to a specialist aphid: eco-evolutionary perspective on genotypic variation and demographic consequences.** *J Ecol* 2015, **103**:809-818.
39. Debarre F, Lenormand T: **Distance-limited dispersal promotes coexistence at habitat boundaries: reconsidering the competitive exclusion principle.** *Ecol Lett* 2011, **14**:260-266.
40. Moreira X, Mooney KA, Zas R, Sampedro L: **Bottom-up effects of host-plant species diversity and top-down effects of ants interactively increase plant performance.** *Proc Roy Soc B* 2012, **279**:4464-4472.
41. Wise MJ, Rausher MD: **Evolution of resistance to a multiple-herbivore community: genetic correlations, diffuse coevolution, and constraints on the plant's response to selection.** *Evolution* 2013, **67**:1767-1779.
42. Utsumi S: **Feeding evolution of a herbivore influences an arthropod community through plants: implications for plant-mediated eco-evolutionary feedback loop.** *J Ecol* 2015, **103**:829-839.
43. Heinen-Kay JL, Noel HG, Layman CA, Langerhans RB: **Human-caused habitat fragmentation can drive rapid divergence of male genitalia.** *Evol Appl* 2014, **7**:1252-1267.
- This is the first study to make the link between habitat fragmentation and rapid divergence of sexually selected genitalia. Genital shape and allometry repeatedly diverged in fragmented locations due to decreased predator density and increased conspecific density.
44. Banks SC, Piggott MP, Stow AJ, Taylor AC: **Sex and sociality in a disconnected world: a review of the impacts of habitat fragmentation on animal social interactions.** *Can J Zool* 2007, **85**:1065-1079.
45. Candolin U, Wong BBM: *Behavioral Responses to a Changing World: Mechanisms and Consequences.* Oxford University Press; 2012.
46. Maan ME, Seehausen O: **Ecology, sexual selection and speciation.** *Ecol Lett* 2011, **14**:591-602.
47. Ritchie MG: **Sexual selection and speciation.** *Ann Rev Ecol Syst* 2007, **38**:79-102.
48. Banks SC, Ward SJ, Lindenmayer DB, Finlayson GR, Lawson SJ: **The effects of habitat fragmentation on the social kin structure and mating system of the agile antechinus, *Antechinus agilis*.** *Mol Ecol* 2005, **14**:1789-1801.
49. Dale S: **Female-biased dispersal, low female recruitment, unpaired males, and the extinction of small and isolated bird populations.** *Oikos* 2001, **92**:344-356.
50. Gibbs JP, Faaborg J: **Estimating the viability of ovenbird and Kentucky warbler populations in forest fragments.** *Conserv Biol* 1990, **4**:193-196.
51. Kokko H, Rankin DJ: **Lonely hearts or sex in the city? Density-dependent effects in mating systems.** *Philos Trans Roy Soc Lond B: Biol Sci* 2006, **361**:319-334.
52. Kvarnemo C, Ahnesjo I: **The dynamics of operation sex ratios and competition for mates.** *Trends Ecol Evol* 1996, **11**:404-408.
53. Klug H, Heuschele J, Jennions MD, Kokko H: **The mismeasurement of sexual selection.** *J Evol Biol* 2010, **23**:447-462.
54. Kokko H, Mappes J: **Sexual selection when fertilization is not guaranteed.** *Evolution* 2005, **59**:1876-1885.
55. Tinghitella RM, Zuk M: **Asymmetric mating preferences accommodated the rapid evolutionary loss of a sexual signal.** *Evolution* 2009, **63**:2087-2098.
56. Zuk M, Kolluru G: **Exploitation of sexual signals by predators and parasitoids.** *Quart Rev Biol* 1998, **73**:415-438.
57. Pfennig KS, Pfennig DW: **Character displacement: ecological reproductive responses to a common evolutionary problem.** *Quart Rev Biol* 2009, **84**:253-276.
58. Jennions MD, Petrie M: **Variation in mate choice and mating preferences: a review of causes and consequences.** *Biol Rev Camb Philos Soc* 1997, **72**:283-327.
59. Zuk M, Rotenberry JT, Tinghitella RM: **Silent night: adaptive disappearance of a sexual signal in a parasitized population of field crickets.** *Biol Lett* 2006, **2**:521-524.