

Wing morphology of a forest damselfly is related to landscape structure

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We demonstrate that, after correcting for the effects of size, the wing lengths, wing widths and thoracic weights of the forest damselfly *Calopteryx maculata* differ between populations along forested streams, and those along streams through pasture. Pasture landscapes can be considered as fragmented forest landscapes; forest landscapes are continuous. In the fragmented landscapes some *C. maculata* fly across intervening pasture to reach foraging sites in forest. We propose that there is morphological plasticity within the species that is revealed through the landscape process of habitat fragmentation and that there is micro-scale selection within the fragmented landscapes for individuals that are better suited to make these flights.

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Habitat fragmentation (Harris and Silva-Lopez 1992) is an ecological process that changes the spatial patterns of habitats in landscapes. It causes a reduction in total habitat area and can isolate resource patches in a matrix of non-resources. Fragmentation alters landscape structure (Dunning et al. 1992, Taylor et al. 1993). It alters the composition of landscapes by removing or adding resource patches (Wilcove et al. 1986, Karr 1990), it alters the configuration of resource patches in landscapes by changing their size, shape and relative positions and through changes to composition and configuration, it can alter landscape connectivity – the ability of animals to move through the landscape to access resources (Wegner and Merriam 1990, Taylor et al. 1993). In spite of extensive forest fragmentation in eastern North America (for example) most species persist (Middleton and Merriam 1983). Gaining insight into how and why individual species persist may assist conservation biologists in predicting the effects of fragmentation on biota and may lead to additional insights into the behavioral ecology and population dynamics of the organisms themselves.

The damselfly *Calopteryx maculata* (P. de Beauvois)

(Odonata: Calopterygidae) inhabits forested streams as nymphs. Adults mate and oviposit along these same streams and forage in the adjacent forest (Johnson 1962, Waage 1973). Normally considered a forest animal (Johnson 1962, Waage 1973) we have found extensive populations of adult *C. maculata* along streams separated from forest habitats by bands of pasture habitat 200–500 m wide. In these fragmented (pasture) landscapes, individuals continue to forage in the now disjunct forest patches by simply flying across the intervening pasture.

A rich literature on morphology of animals and flight (Harrison 1980, Wootton 1992) shows a clear relationship between the degree of wingedness (whether animals have no, short, or long wings) and the stability or isolation of habitats (Wagner and Liebherr 1992). In the Gerriidae for example, winged and non-winged forms exist within the same species, but long-winged forms utilize temporal stream habitats that occasionally dry up (Kaitala and Dingle 1992). Conversely, the evolution of flightlessness in insect species on islands suggests that where flight is a disadvantage it quickly disappears within populations (Wagner and Liebherr 1992). Most studies of differences

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in morphology associated with flight have focused on the relationship between these discrete and recognizable wing polymorphisms and patterns of migration or dispersal movements (Harrison 1980). The numerous examples of positive relationships between flight ability and habitat suggest that more subtle differences in wing morphology might be selected for in individuals of the same species that live in habitats with different energetic costs and constraints. For example, Kodric-Brown and Brown (1978) suggest that females of the hummingbird *Selasphorus rufus* forage at more sparsely distributed flowers than do males because their longer wings permit more efficient flight, and Dempster (1991) shows that thoracic shape in some British Lepidoptera has changed during time periods when the distribution of their habitat within landscapes was being altered.

Here we examine how wing morphology (wing length and width) and thoracic mass of *C. maculata* differ between forest (continuous) and pasture (fragmented) landscapes. We first show that the distribution of *C. maculata* in the two types of landscape differs and then test the hypothesis that morphological attributes associated with flight (i.e. wing morphology and thoracic mass) differ between the two landscapes in a manner consistent with the differences in distribution.

Methods

Study areas

Surveys were conducted north of Ottawa, Canada (45°20'N; 75°40'W) in a rolling landscape of pasture and forest. The area consists of granitic outcrops interdigitated with valleys. Valley bottoms are predominantly pasture (cleared circa 165 yr ago) actively grazed by cattle, and adjacent hillsides are covered in deciduous forest. *C. maculata* is abundant along many of the small streams that flow from lakes on the outcrops into the valleys.

C. maculata were observed and collected at three SITES¹: Drury (UTM²: 18VF 288 490), Eardley (UTM: 18VF 150 465) and Masham (UTM: 18VF 182 601). Each SITE had both a forest and pasture LANDSCAPE. A forest LANDSCAPE contained forest habitat immediately adjacent to streams. A pasture LANDSCAPE comprised both forest and pasture habitats. In pasture landscapes, alder (*Alnus incana* (L.) Moench) bordered the streams and the nearby hillsides were forested. These forest patches were separated from the edge of the stream by a 200–500 m wide band of pasture habitat. Streams varied in width from 1–2 m. At Drury and Eardley, the streams flowed first through forest, then pasture. At Masham one stream flowed through forest and joined a larger stream flowing through pasture. All streams flowed throughout the duration of the study.

Distribution of individuals

To assess whether the distribution of *C. maculata* in the habitats adjacent to the streams differed between LANDSCAPES, we conducted a series of transect surveys in both types of LANDSCAPE at two SITES (Masham and Drury). A transect consisted of walking at a steady pace perpendicular to the stream for 600 m counting and sexing all *C. maculata* observed in each of 25, 24-m long sections. In the forest landscapes, transects were completely within forest habitat. In the pasture landscapes, transects first traversed 200–500 m of pasture habitat, then traversed forest habitat. A minimum of 14 transects were traversed in each LANDSCAPE at each SITE (balanced by month and time of day). We tested the effect of landscape type on the mean distance from the edge of the stream that damselflies were observed by fitting an ANOVA model with the main effects: LANDSCAPE, SEX and SITE (plus all interactions).

Collections

Collections were made between 10.45 and 12.00 using a standard insect net. Thoracic mass varies with age (Anholt et al. 1991) so to reduce this variability we only collected individuals at or immediately next to streams. These individuals are predominately territorial males and females ready to oviposit (Waage 1972, Forsyth and Montgomerie 1987) and so have undergone a maturation period of about 7 d (Waage 1972). When individuals that were obviously recently emerged (these have smoky-grey wings and brown eyes) were encountered we did not collect them.

We collected 5 individuals of each SEX from each pair of LANDSCAPES at a single SITE, on a single collecting day. Collections from the three sites were made on successive days within the MONTHS of June and July and all collections were made within a single flight season (1992). The original design is completely balanced: 2 SEXES × 3 SITES × 2 LANDSCAPES × 2 MONTHS (nested within SITE) for a total of 120 individuals but 2 individuals were subsequently lost.

Morphological measurements

The right forewing was clipped at its base from each individual and the wing was placed between two microscope slides. WING LENGTH was measured from the base of the arculus to the tip of the wing beneath the pterygium (in males, just above the point where vein R1 intersects with the wing margin). WING WIDTH was measured along a perpendicular line from the nodus. Allometrically, larger individuals will have bigger wings (Wootton 1992) so we also measured the length of the femur on the right foreleg as an overall size covariate. In a few cases the right wing or foreleg was damaged or missing so the left wing or foreleg was measured instead. Three individuals had femur measurements that were clearly erroneous (> 3

¹ Throughout the text, factor names included in statistical models are in a SMALL CAPS font.

² UTM – Universal Transverse Mercator grid system.

Table 1. Analysis of variance table. The response variable is the square root of the distance from the edge of streams that *Calopteryx maculata* were observed during transect surveys.

	df	Mean Square	F	p(F)
SITE	1	1.57	0.82	0.37
SEX	1	11.17	5.82	0.17
LANDSCAPE	1	15.16	7.90	0.006
SITE × SEX	1	2.03	1.06	0.31
SITE × LANDSCAPE	1	0.03	0.01	0.90
SEX × LANDSCAPE	1	4.44	2.32	0.13
SITE × SEX × LANDSCAPE	1	0.22	0.12	0.73
Residual	168	1.92		

standard errors from the mean). So as not to further reduce the balance of the design, these measurements were dropped, and new measures estimated from a linear model fit using the main treatment variables in the survey (SEX, SITE, LANDSCAPE, and MONTH nested within SITE).

Measurements were repeated blind on 30 (20%) specimens to get an independent estimate of measurement error. 27/30 (90%) of the check measurements were <2.4% (0.6 mm) of the initial measurement (average 1.4%). The measurer was blind to knowledge of the origin of the wings (i.e. forest or pasture landscapes).

Thoraces were stripped of wings, heads and all appendages, dried for 72 h at 50°C (until stable weights were reached) and weighed (± 0.1 mg).

Statistical methods

Our aim was to test whether wing morphology and thoracic mass were related to landscape structure. Wing morphology and thoracic mass will be related to the size that an individual attains as a larva, which in turn will be dependent upon the environmental conditions in the stream within which it lives (Anholt 1990). Therefore, in all our statistical models, we needed to first eliminate these contributions of SIZE before testing for effects of landscape structure. However, since SIZE itself may be

Table 2. Analysis of variance table. The response variable is the femur length (size) of *Calopteryx maculata* from forest and pasture landscapes. Residuals from this model are used as an independent variable (SIZE RESIDUALS) in models 2 and 3 (Table 3, 4).

	df	Mean Square	F	p(F)
SITE	2	0.02	0.19	0.83
SEX	1	1.14	11.82	<0.001
LANDSCAPE	1	0.25	2.59	0.11
MONTH {IN} SITE	3	0.19	1.94	0.13
SITE × SEX	2	0.06	0.62	0.54
SITE × LANDSCAPE	2	0.18	1.84	0.16
SEX × LANDSCAPE	1	0.09	0.90	0.34
SEX × (MONTH {IN} SITE)	3	0.21	2.19	0.09
(MONTH {IN} SITE) × LANDSCAPE	3	0.07	0.28	0.54
Residual	99	0.10		

influenced by the independent variables of interest (SEX, SITE, LANDSCAPE and MONTH), including it may obscure the relationship between these variables and the morphological variables. Therefore, we eliminated the influence of these independent variables on SIZE by fitting a statistical model including SEX, SITE, LANDSCAPE and MONTH nested within SITE (plus two-way interactions) to SIZE and used the residuals from this model as a new measure of SIZE. For the same reasons, we used the residuals from models of wing morphology to test for the effects of wing width and wing length on thoracic mass.

All statistical models presented are ANOVA models, fit using the glm procedure in Splus (Chambers and Hastie 1992). Residuals are deviance residuals (McCullagh and Nelder 1989). In all models we assessed the adequacy of fit by examining plots of residuals versus fitted and residuals versus predicted values.

Results

Differences in distribution

176 individual *C. maculata* were observed on transects. On average, they were found significantly farther from the edge of the stream in pasture LANDSCAPES than in forest LANDSCAPES ($\bar{x} \pm SE$ distance from the edge of the stream: pasture: 284 ± 5 m, forest: 189 ± 3 m; Table 1, LANDSCAPE effect) and the difference was consistent across the two SITES (Table 1, no LANDSCAPE × SITE interaction). In pasture landscapes, *C. maculata* were only rarely (3/62 observations) observed within the pasture habitat; all were observed while flying to or from the forest.

Differences in size

Female *C. maculata* were significantly larger than males (Table 2, p(F) < 0.001). No other factors significantly influenced size.

Differences in wing morphology

WING LENGTH and WIDTH were both dependent upon SIZE, SEX and LANDSCAPE (Table 3). Larger individuals have longer and wider wings (all else being equal), and after correcting for the effects of size, female *C. maculata* have relatively shorter and wider wings than males. These differences are consistent among both months and sites (Table 3, no SITE or MONTH in SITE effect). Individuals from pasture LANDSCAPES have significantly longer and wider wings than those from forest LANDSCAPES. The mean WINGLENGTH of females is 2.5 mm greater than males, and the mean winglength of individuals in pasture is greater than those in forest (females, 0.75 mm; males, 0.89 mm; Fig. 1).

Differences in thoracic mass

All factors contributed significantly to explaining variance in thoracic mass (Table 4). Males had heavier thoraces than females, and larger individuals with longer and

Table 3. Analysis of variance table. Two models are shown. The response variables are wing length and wing width of male and female *Calopteryx maculata* from forest and pasture landscapes at three sites. SIZE RESIDUALS are standardized residuals from the model in Table 2. Residuals from these models are used as independent variables in Table 4.

	df	Wing length			Wing width		
		Mean Square	F	p(F)	Mean Square	F	p(F)
SIZE RESIDUALS	1	13.60	12.22	<0.0001	3.14	20.13	<0.0001
SITE	2	1.33	1.19	0.31	0.19	1.21	0.30
SEX	1	161.60	145.20	<0.0001	0.43	2.77	0.10
LANDSCAPE	1	19.83	17.82	<0.0001	1.00	6.43	0.01
MONTH {IN} SITE	3	3.98	3.58	0.17	0.27	1.70	0.17
SIZE RESIDUALS × SITE	2	0.95	0.85	0.43	0.12	0.80	0.43
SIZE RESIDUALS × SEX	1	0.92	0.82	0.37	0.34	2.21	0.14
SIZE RESIDUALS × LANDSCAPE	1	0.70	0.63	0.43	0.31	1.98	0.16
SITE × SEX	2	0.00	0.00	1.00	0.06	0.38	0.68
SITE × LANDSCAPE	2	2.75	2.47	0.09	0.53	3.37	0.04
SEX × LANDSCAPE	1	0.19	0.17	0.68	0.04	0.27	0.60
(MONTH {IN}) × SIZE RESIDUALS	3	1.99	1.79	0.16	0.06	0.41	0.75
(MONTH {IN}) SITE × SEX	3	1.52	1.36	0.26	0.13	0.86	0.47
(MONTH {IN}) SITE × LANDSCAPE	3	1.27	1.15	0.34	0.01	0.07	0.97
Residual	91	1.11			0.16		

wider wings were heavier. Animals from pasture landscapes had heavier thoraces than those from forest landscapes but the effects were inconsistent across SITES (i.e. there was a significant SITE × LANDSCAPE interaction).

Discussion

C. maculata were found, on average, further from the edges of streams in the pasture landscapes. The result is a function of two factors: a) *C. maculata* were only observed in pasture habitat as transients (i.e. they were not observed in the pasture habitats foraging or resting) and b) in pasture landscapes they continue to use forest habitat for foraging, which is more distant from the stream

edge than it is in forest landscapes. To move between the forest patches and the stream edge in the pasture landscapes, *C. maculata* traverse the pasture habitat. The configuration of resource patches differs between the two landscapes and as a consequence, the damselfly's ecological neighbourhood (sensu Addicott et al. 1987) is expanded. In other words, in pasture landscapes, *C. maculata* move over a larger spatial area.

Flight is an essential component of the behaviour of *C. maculata*. It is used to move between stream and forest for foraging and it is also used by males in elaborate displays to defend territories and to secure females for mating (Johnson 1962). A reasonable hypothesis is that selection in both landscapes will be for morphological traits that facilitate the main components of flight

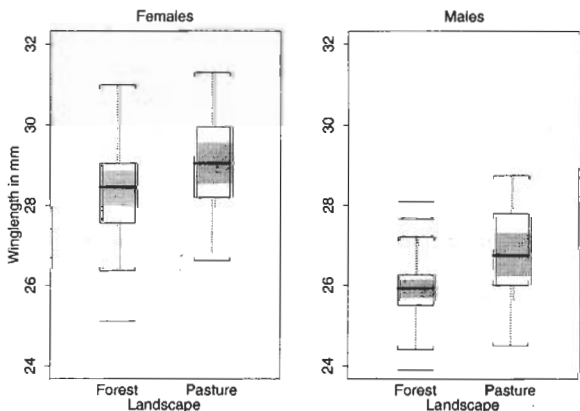
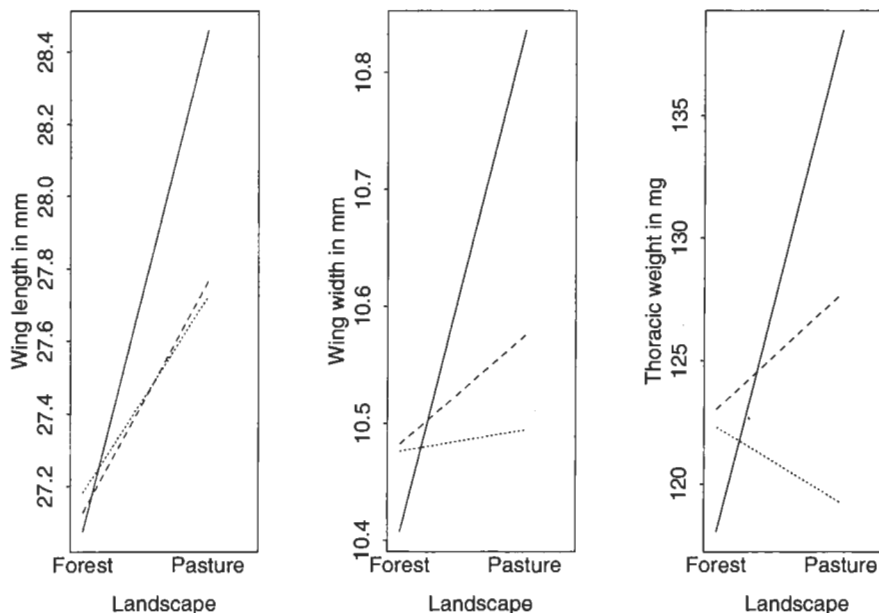


Fig. 1. Boxplots showing median (black bar) ± standard error (shaded), interquartile range (box), range (whiskers) and outliers (bars) of the wing length (mm) of female and male *Calopteryx maculata* in forest and pasture landscapes.

Table 4. Analysis of variance table. The response variable is the thoracic mass of male and female *Calopteryx maculata* collected from forest and pasture landscapes at three sites. SIZE, WING LENGTH and WING WIDTH RESIDUALS are the standardized residuals from the models in Tables 2 and 3.

	df	Mean Square	F	p(F)
SIZE RESIDUALS	1	2763.82	30.43	<0.001
WING LENGTH RESIDUALS	1	3585.87	39.48	<0.001
WING WIDTH RESIDUALS	1	1469.15	16.18	<0.001
SITE	2	665.87	7.33	0.001
SEX	1	1538.67	16.94	<0.001
LANDSCAPE	1	1548.78	17.05	<0.001
MONTH{IN}SITE	3	1272.09	14.01	<0.001
SITE × SEX	2	444.66	4.90	0.009
SEX × LANDSCAPE	1	117.93	1.30	0.257
SITE × LANDSCAPE	2	1382.76	15.23	<0.001
(MONTH{IN}SITE) × LANDSCAPE	3	132.65	1.46	0.230
(MONTH{IN}SITE) × sex	3	517.72	5.70	0.001
Residual	94	90.82		

Fig. 2. Interaction plots showing mean wing length (mm), mean wing width (mm) and mean thoracic mass (mg) of *Calopteryx maculata* in forest and pasture landscapes among three sites: Masham – solid line, Eardley – dashed line, Drury – dotted line.



within the environmental constraints peculiar to that type of landscape. Our results are consistent with this hypothesis. *C. maculata* from the two types of landscape have significant morphological differences associated with flight. In pasture landscapes they are larger, have heavier thoraces, and longer and wider wings than they do in forest landscapes. The differences in sizes of individuals from pasture and forest landscapes may at first suggest that the larger-winged individuals in pasture result from a better growth environment for larvae in pasture streams (e.g. more food or more degree days for development due to altered micro-environmental conditions). The residual effect of size in both sets of models shows that this is partly true. However, after accounting for this effect, pasture individuals still have longer and wider wings, and heavier thoraces, suggesting that a more fundamental morphological difference exists between *C. maculata* inhabiting the two kinds of landscapes. Such a difference might arise through selection for morphological characteristics that improve flight in the two landscapes, through selection for wing morphologies more amenable to (possible) differences in reproductive behaviours in the two landscapes, or through a more complex relationship between environment, morphology and behavior than can be teased out in these analyses.

Current knowledge of the relationship between wing morphology and flight abilities of different kinds is slim, but in principal, larger wings will produce more lift and carry heavier loads (Marden 1987, Wootton 1992). Marden (1987) showed that most of the variance in the ability of insects to lift increased weights was related to flight muscle mass (a major component of thoracic mass) and little additional variance could be explained by wing area. However, Marden (1987) points out that longer wings

may be more advantageous for *forward* flight and Wootton (1992) suggests that longer, more slender wings may improve the efficiency of *prolonged* flight. *C. maculata* from pasture landscapes had slightly more slender wings than those from forest landscapes (mean (\pm SE) ratios of wing width to length: 0.381 ± 0.002 in pasture vs 0.386 ± 0.002 in forest; $p = 0.035$, ANOVA, with sex and landscape as factors).

If the additional movement required by individuals living in the pasture landscape is the force selecting for observed differences in wing morphology and thoracic mass, it should do so depending on the configuration of habitats within sites. Since pasture landscapes will be more variable than forest landscapes (streams are immediately adjacent to forest in all forest landscapes by definition) we would expect to see larger differences between the pasture landscapes, among sites, than between the forest landscapes (i.e. a SITE \times LANDSCAPE interaction). There is evidence for such an interaction (SITE \times LANDSCAPE in: WING LENGTH model; $p = 0.09$; WING WIDTH model; $p = 0.04$; THORACIC model; $p < 0.0001$) in our statistical models and plots of each of the three interactions (Fig. 2) show that indeed the largest differences are consistently within the pasture landscapes across the three sites.

Differences in the configuration of resource patches might also influence patterns of feeding, so as Anholt (1991) suggests, selection for behavioral characteristics might be reflected in differences in morphology or resource allocation in the two types of landscapes. Such differences might also be reflected by, or be a consequence of, different patterns of change in mating strategy. We did not study differences in mating behaviours between populations in the two types of landscape. How-

ever, *C. maculata* has been shown to alter its mating strategy as it ages (Forsyth and Montgomerie 1987) and Marden and Waage (1990) showed that the ability of males to successfully defend territories was dependent upon energy reserves (a component of thoracic mass) which has been shown to vary with age (Anholt et al. 1991).

Whether changes in wing morphology are proximately caused by habitat fragmentation is unknown. Our results indicate that there is morphological plasticity within the species that is revealed in response to habitat fragmentation and the mechanisms we suggest are consistent with patterns of distribution and behaviour in *C. maculata* in forest and pasture landscapes. Genetically based phenotypic-plasticity has been shown in other insect species in response to different environments (Blanckenhorn 1991) and wing morphology has been shown to differ between races of an American wood warbler (*Dendroica townsendi*) that have different migration distances (Morrison 1983). The speed and direction of the changes in response to changes in landscapes are generally unknown, but Dempster (1991) has shown that morphological change in several species of Lepidoptera (possibly in response to changing configurations of habitat) can occur quite rapidly (within 10 yr). Collectively, these data suggest that morphological plasticity associated with movement may be an important component to the survival or demise of some animal populations in rapidly changing environments.

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References

- Addicott, J. F., Aho, J. M., Antolin, M. F., Padilla, D. K., Richardson J. S. and Soluk, D. A. 1987. Ecological neighbourhoods: scaling environmental patterns. – *Oikos* 49: 340–346.
- Anholt, B. R. 1990. Size-biased dispersal prior to breeding in a damselfly. – *Oecologia* 83: 385–387.
- 1991. Measuring selection on a population of damselflies with a manipulated phenotype. – *Evolution* 45: 1091–1106.
- , Marden, J. H. and Jenkins, D. M. 1991. Patterns of mass gain and sexual dimorphism in adult dragonflies (Insecta: Odonata). – *Can. J. Zool.* 69: 1156–1163.
- Blanckenhorn, W. U. 1991. Life-history differences in adjacent water strider populations: Phenotypic plasticity or heritable responses to stream temperature? – *Evolution* 45: 1520–1525.
- Chambers, J. M. and Hastie, T. 1992. Statistical models in S. – Wadsworth & Brooks, Pacific Grove, CA.
- Dempster, J. P. 1991. Fragmentation, isolation and mobility of insect populations. – In: Collins, N. M. and Thomas, J. A. (eds), *The conservation of insects and their habitats*. Academic Press, London.
- Dunning, J. B., Danielson, B. J., Pulliam, H. R. 1992. Ecological processes that affect populations in complex landscapes. – *Oikos* 65: 169–175.
- Forsyth, A. and Montgomerie, R. D. 1987. Alternative reproductive tactics in the territorial damselfly *Calopteryx maculata*: sneaking by older males. – *Behav. Ecol. Sociobiol.* 21: 73–81.
- Harris, L. D. and Silva-Lopez, G. 1992. Forest fragmentation and the conservation of biological diversity. – In: Fiedler, P. L. and Jain, S. K. (eds), *Conservation biology: the theory and practice of nature conservation, preservation, and management*. Chapman & Hall, London.
- Harrison, R. G. 1980. Dispersal polymorphisms in insects. – *Annu. Rev. Ecol. Syst.* 11: 95–118.
- Johnson, C. 1962. Breeding behaviour and oviposition in *Calopteryx maculatum* (Beauvois) (Odonata: Calopterygidae). – *Am. Midl. Nat.* 68: 242–247.
- Kaitala, A. and Dingle, H. 1992. Spatial and temporal variation in wing dimorphism of California populations of the water-strider *Aquarius remigis* (Heteroptera: Gerridae). – *Ann. Entomol. Soc. Am.* 85: 590–595.
- Karr, J. R. 1990. Avian survival rates and the extinction process on Barro Colorado Island, Panama. – *Cons. Biol.* 4: 391–397.
- Kodric-Brown, A. and Brown, J. H. 1978. Influence of economics, interspecific competition, and sexual dimorphism on territoriality of migrant rufous hummingbirds. – *Ecology* 59: 285–296.
- Marden, J. H. 1987. Maximum lift production during takeoff in flying insects. – *J. Exp. Biol.* 130: 235–258.
- and Waage, J. K. 1990. Escalated damselfly territorial contests are energetic wars of attrition. – *Anim. Behav.* 39: 954–959.
- McCullagh, P. and Nelder, J. A. 1989. *Generalized linear models*. – Chapman & Hall, London.
- Middleton, J. and Merriam, G. 1983. Distribution of woodland species in farmland woods. – *J. Appl. Ecol.* 20: 625–644.
- Morrison, M. L. 1983. Analysis of geographic variation in the Townsend's Warbler. – *Condor* 85: 385–391.
- Taylor, P. D., Fahrig, L., Henein, K. and Merriam, G. 1993. Connectivity is a fundamental element of landscape structure. – *Oikos* 68: 571–573.
- Waage, J. K. 1972. Longevity and mobility of adult *Calopteryx maculata* (Beauvois, 1805) (Zygoptera: Calopterygidae). – *Odonatologica* 1: 155–162.
- 1973. Reproductive behavior and its relation to territoriality in *Calopteryx maculata* (Beauvois) (Odonata: Calopterygidae). – *Behaviour* 48: 240–256.
- Wagner, D. L. and Lieberr, J. K. 1992. Flightlessness in insects. – *Trends Ecol. Evol.* 7: 216–220.
- Wegner, J. and Merriam, G. 1990. Use of spatial elements in a farmland mosaic by a woodland rodent. – *Biol. Conserv.* 54: 263–276.
- Wilcove, D. S., McLellan, C. H. and Dobson, A. P. 1986. Habitat fragmentation in the temperate zone. – In: Soulé, M. E. (ed.), *Conservation biology: The science of scarcity and diversity*. Sinauer, MA, pp. 237–256.
- Wootton R. J. 1992. Functional morphology of insect wings. – *Annu. Rev. Entomol.* 37: 113–40.