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Flight morphology in fragmented populations of a rare British butterfly, *Hesperia comma*

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Abstract

In modern landscapes, many populations of rare species are restricted to fragments of formerly extensive habitat. However, the potential for evolutionary changes in dispersal ability to occur within these fragmented populations has received little attention. We examined morphological traits associated with flight and reproduction in fragmented populations of the silver-spotted skipper butterfly, *Hesperia comma*. Investment in flight was measured as relative wing area and thorax mass, and investment in reproduction as relative abdomen mass. All measurements were made on individuals reared in a common environment. In the UK, *Hesperia comma* was once fairly widely distributed in southern and eastern England, but retracted to its smallest UK distribution in the 1970s and 1980s. It then partially re-expanded in the North and South Downs in S.E. England. We first compared traits from colonised and refuge sites 2.9–4.5 km apart, and found no differences in relative investment in flight or reproduction. There were, however, significant differences in both relative thorax and abdomen mass between regions >40 km apart. Populations with the highest relative investment in the thorax occurred in a region where population expansion has been most rapid. These results, in combination with other studies linking butterfly morphology to patch area and/or isolation, suggest that evolutionary responses to habitat fragmentation could be widespread. © 1998 Elsevier Science Ltd. All rights reserved.

Keywords: Colonisation; Dispersal; Distribution; Isolation; Metapopulation

1. Introduction

Worldwide destruction of natural habitats has led to the isolation of many populations of rare and endangered species and has resulted in many populations being restricted to ‘islands’ of formerly extensive habitat (e.g. Groombridge, 1992). Adaptations of endemic species on true, oceanic islands have shown that isolation has important consequences for the evolution of dispersal ability (e.g. Williamson, 1981). However, evolutionary changes in dispersal traits in populations in fragmented landscapes have received little attention (Thomas et al., 1998).

In highly fragmented landscapes, isolated populations may evolve traits associated with low dispersal if emigrants from isolated patches are not replaced by immigrants, and if emigrants represent a genetically non-random component of the population. Some evidence for evolutionary changes in isolated populations comes from museum specimens of the swallowtail butterfly *Papilio machaon* L. and the large blue butterfly *Maculinea arion* (L.), where changes in thorax shape may indicate weaker flight ability in isolated populations (Dempster et al., 1976; Dempster, 1991). However, most rare butterflies persist as metapopulations rather than as single isolated populations (Thomas and Hanski, 1997), and empirical evidence is lacking for evolutionary changes in dispersal rates in metapopulations that occupy landscapes of different levels of fragmentation.

Theoretical models predict that altered rates of colonisation and extinction could drive evolutionary changes in dispersal rates within metapopulations: dispersal is favoured during colonisation but may be at a selective disadvantage within each population once it has been founded (Olivieri et al., 1995; Olivieri and Gouyon,

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1997). Support for these predictions comes from empirical studies of beetles and plants which show that dispersal traits may decline rapidly in newly established populations, and that colonisation of empty habitats may result in an increase in dispersal traits (Den Boer, 1970; Nielmela and Spence, 1991; Cody and Overton, 1996).

In this paper, we examine morphological traits associated with dispersal in the patchily distributed silver-spotted skipper butterfly, *Hesperia comma* L., in three metapopulations which inhabit landscapes that differ in their degree of fragmentation. The morphological traits that we measured were relative investment in wing area, thorax mass and abdomen mass. Insect dispersal ability has been related to adult morphology (Palmer and Dingle, 1989; Fairbairn and Roff, 1990), typically with a trade-off between flight and reproduction (Zera and Denno, 1997). Butterfly flight speed is positively correlated with wing span (Dudley, 1990), thorax mass (principally flight muscle mass; Srygley and Chai, 1990) and thorax width (Dempster et al., 1976; Chai and Srygley, 1990) while relative abdomen mass (containing reproductive organs, as well as storage organs and haemolymph) is negatively related to flight speed (Srygley and Chai, 1990). We compared morphological traits at two spatial scales; between local populations (< 5 km apart) within metapopulations, and between metapopulations (> 40 km apart) which differ in degree of habitat fragmentation and colonising history (which we also document).

2. Materials and methods

2.1. Study species

Hesperia comma was once fairly widely distributed on short-grass calcareous grasslands in southern and eastern England (Thomas et al., 1986) but, by 1982, had declined to just 46 populations in 10 regions. This decline occurred during a period of reduced grazing levels, resulting mainly from declining rabbit populations *Oryctolagus cuniculus* L. due to the introduction of myxomatosis in the 1950s (Smith, 1980). A few large silver-spotted skipper populations survived, however, in refuges where domestic grazing continued or succession was very slow. Over the past 20 years, recovery of rabbit populations and appropriate habitat management have restored short-grass habitats to many areas, and skipper populations have recolonised some areas. Nonetheless, many formerly occupied habitats have failed to be repopulated (Thomas and Jones, 1993).

2.2. Spatial structure of habitat and distribution of H. comma

The distribution of *H. comma* was surveyed in two ranges of chalk hills in S.E. England, the North and South Downs, in 1982 and 1991 (Thomas and Jones, 1993). The entire area was searched, locating every patch of suitable breeding habitat and searching for adults and eggs. Habitat patches were recognised as separate from one another if they were divided by a continuous barrier of woodland or scrub, or by at least 25 m of unsuitable grassland (Thomas and Jones, 1993). Populations survived in four regions along the North and South Downs (Fig. 1; Thomas and Jones, 1993) and we studied three of these (Surrey, East Sussex and Hampshire) in more detail. Distribution maps (Fig. 1) were drawn to include all occupied patches (see Thomas and Jones, 1993). Data from Thomas and Jones (1993) were re-analysed for the three regions from which we also obtained material for morphological studies (see below; Table 1).

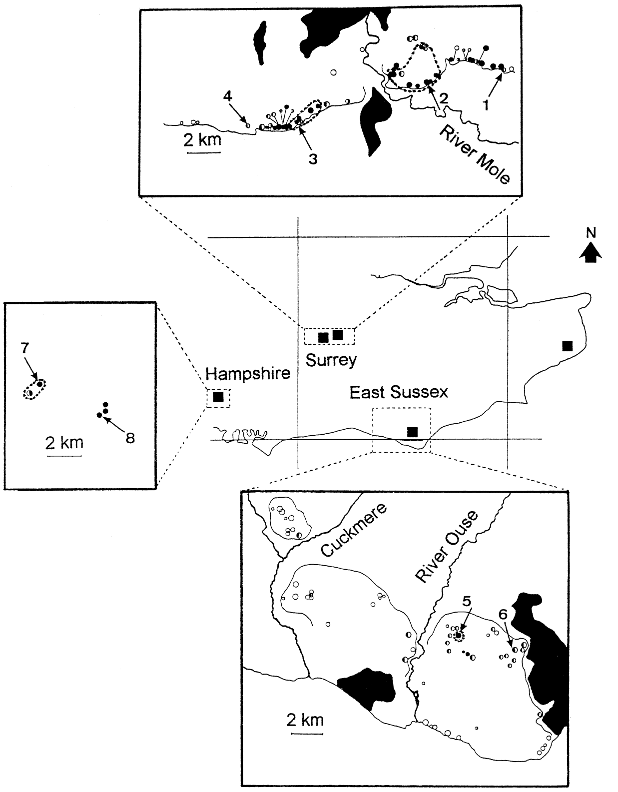

Fig. 1. Distribution of *H. comma* (■) along the North and South Downs in S.E. England. Three areas (Surrey, East Sussex and Hampshire) are shown in more detail. The entire area was surveyed in 1982 and 1991. ● = patches occupied in both years, ◐ = presumed colonisation (present 1991 only), ◑ = presumed extinction (present 1982 only); ○ = patches of suitable habitat vacant both years. In all cases, size of symbol represents area of habitat patch: small symbol ⩽0.1 ha; medium = 0.11–0.99 ha; large ⩾ 1.0 ha. Thin solid lines indicate limit of chalk downland, shading shows urban areas and areas enclosed by dotted lines indicate presumed refuge areas. Nine circles represent multiple sites (either two or three patches, total = 21 sites) which are less than 80 m apart. Arrows indicate sampling sites; 1, Reigate Hill; 2, Brockham Warren Quarry; 3, White Downs Quarry; 4, Colekitchen Farm; 5, Deepdene; 6, Combe Hill; 7, Beacon Hill; 8, Old Winchester Hill.

Table 1
Spatial distribution of habitat in three regions in S.E. England

	Surrey	East Sussex	Hampshire
Habitat structure			
Number of patches	69	54	6
Log patch area (ha)	x = −0.48a SD = 0.67	x = −0.33a SD = 0.60	x = 0.56b SD = 0.26
Log dist. between patches (m)	x = 1.87a SD = 0.52	x = 2.23b SD = 0.46	x = 2.40ab SD = 0.18
% patches occupied in 1982	69.6	5.6	(4 patches)
Colonization/extinction			
% patches colonized	17.4	35.2	0
Log colonization dist. (m)	x = 2.05a SD = 0.53	x = 2.59b SD = 0.70	–
Max. colonization dist. (m)	600	8650	–
% patches extinct	10.1	0	(1 patch)
Vacant patches			
% patches vacant in both years	13.0	59.3	(1 patch)
Log dist. to nearest occupied patch (m)	x = 2.89a SD = 0.69	x = 3.61b SD = 0.42	3.79
Log patch area (ha)	x = −1.04a SD = 0.72	x = −0.50b SD = 0.52	0.95
Refuge patches			
Number of patches	15?	1	2
Patch area (ha)	x = 0.96 SD = 0.96	18.0	x = 4.50 SD = 2.97

129 patches of suitable breeding habitat were identified and presence/absence of *H. comma* recorded in 1982 and 1991. Data were re-analysed from Thomas and Jones (1993). Means followed by a different letter are significantly different at the 5% level using *t*-tests or ANOVA and Tukey tests on $\log_{10}$-transformed data. x = mean, SD = standard deviation.

In Surrey (Fig. 1), refuge populations survived in two areas where succession would have been very slow in quarries and on other skeletal soils, and in one location where trampling kept the sward short [Thomas and Jones, 1993; Biological Records Centre (BRC), Institute of Terrestrial Ecology, Monks Wood; K. Willmott, G. Collins and G. Jeffcoate, pers. comm.]. In East Sussex, one population persisted at Deepdene, where domestic grazing continued throughout the 1970s to the present day. In Hampshire, *H. comma* persisted at Beacon Hill, and probably also at Winter's Down just to the south-west until the early 1980s, but had gone extinct at Winter's Down by 1991 (BRC; Thomas and Jones, 1993). Old Winchester Hill was occupied until the 1950s when grazing was stopped and the population went extinct.

2.3. Rearing and flight morphology

H. comma eggs were collected from eight sites in Surrey, East Sussex and Hampshire during September 1995 (Fig. 1). Sites were chosen in pairs to include a refuge site (R) and a colonised site (C). There were four sites in Surrey: White Downs Quarry (R), Colekitchen Farm (C), Brockham Warren Quarry (R), and Reigate Hill (C); two sites in East Sussex: Deepdene (R) and Combe Hill (C); and two sites in Hampshire: Beacon Hill (R) and Old Winchester Hill (C). Colekitchen Farm, Reigate Hill and Combe Hill, were (re)colonised between 1982 and 1991 (Thomas and Jones, 1993) and Old Winchester Hill was re-colonised in the 1970s (Thomas et al., 1986). Eggs were placed on potted *Festuca ovina* L. plants, covered with fine netting and placed outside in a sheltered position over winter. Plants with eggs were placed in a screen house in spring, checked regularly and larvae transferred to new plants when necessary. On pupation, pupae were returned to the laboratory and placed in individual containers. Adults were frozen within 24 h of emergence and subsequently thawed, dissected under a microscope, and dried to constant mass at 60°C for 24 h. Body parts (thorax, abdomen, wings, head and legs) were weighed on a Cahn Electrobalance (sensitivity 0.1 μg). Wings were mounted on glass microscope slides and their areas and lengths measured using an image analysis system (TAS software, University of Leeds). All variables were $\log_{10}$-transformed for analysis and these transformed variables did not differ significantly from normal ($p > 0.2$ in all cases).

3. Results

3.1. Spatial structure of habitat

The distribution of habitat patches differed between regions, although the small number of patches in Hampshire ($n = 6$) meant that data for this region were not included in subsequent analyses. Habitat patch areas did not differ significantly between Surrey and East Sussex but patches were further apart in East Sussex (Table 1). Compared with Surrey, a larger percentage of patches was colonised in East Sussex between 1982 and 1991 and colonisation distances were longer, with a maximum colonisation distance of 8650 m recorded in East Sussex but only 600 m in Surrey. A smaller percentage of patches remained vacant in Surrey, but vacant sites were closer to occupied sites and were smaller than in East Sussex (Table 1). The distribution of refuge sites also differed between regions, with East Sussex having one large refuge site but Surrey having approximately 15–20 smaller sites.

3.2. Morphology

We collected similar numbers of eggs from each site, and although we did not measure mortality rates directly, survival of hatched eggs was similar among regions. A total of 57 adults (36 males, 21 females) was measured, although a few adults did not completely expand their wings on emergence and so sample sizes for wing-related traits are smaller than those for other measures. Wing lengths of specimens (mean = 14.5 mm) were very similar to those of wild adults (14–16 mm; Emmet and Heath, 1990) indicating that growth was similar to that in the wild. There were no significant differences among regions (Surrey, East Sussex and Hampshire) in total dry mass (Table 2, ANOVA with sex and region as factors and colonisation/refuge nested within region; $F_{2,50} = 1.51$, $p = 0.23$) or adult emergence date ($F_{2,50} = 0.12$, $p = 0.89$), indicating that development rates did not differ among populations, although males were smaller ($F_{1,50} = 233.87$, $p < 0.001$) and emerged earlier ($F_{1,50} = 9.12$, $p = 0.004$). Males also had smaller wing loadings (total dry mass/wing area; $F_{1,46} = 72.34$, $p < 0.001$), but there were no significant differences among regions in either wing loading ($F_{2,46} = 0.06$, $p = 0.94$) or aspect ratio (wing span^2/wing area; $F_{2,46} = 1.72$, $p = 0.19$).

3.3. Relative investment in wings and thorax

Table 2 gives summary data of morphology measurements of specimens from the three regions. However, absolute measures of thorax, abdomen and wing area do not take account of effects of allometry, and so relative investment in different body parts was analysed by calculating residual values. The slopes of the relationships between total body mass and either thorax mass or wing area did not differ significantly among regions (ANCOVA with sex and region as factors and total mass as a covariate; thorax, $F_{2,49} = 0.26$, $p = 0.78$; wing, $F_{2,45} = 0.55$, $p = 0.58$) or between sexes (thorax, $F_{1,49} = 0.28$, $p = 0.60$; wing, $F_{1,45} = 0.01$, $p = 0.94$). Residuals were calculated for each individual from regressions of wing area and thorax mass on total mass (separate regressions for each sex) to produce two indices of relative investment in flight. There were significant differences among regions in relative thorax mass ($F_{2,50} = 3.29$, $p = 0.045$), with individuals from East Sussex having relatively large thoraxes and individuals from Surrey having relatively small thoraxes (Fig. 2). These differences in residual values correspond to c. 13% increase in thorax mass for males and c. 10% increase in thorax mass for females from populations in East Sussex compared with populations in Surrey (Table 2). Differences in *relative* size are the crucial consideration, but absolute values give an indication of the scale of differences involved. Relative wing area did not differ significantly among regions (ANOVA with

Table 2
Morphology measurements of adult *H. comma* from Surrey ($n = 11$ males, eight females), East Sussex ($n = 10$ males, nine females) and Hampshire ($n = 15$ males, four females)

		Surrey		East Sussex		Hampshire	
		Mean	SD	Mean	SD	Mean	SD
Total dry mass (mg)	M	27.32	3.06	28.94	3.47	28.62	3.21
	F	43.96	5.28	46.33	3.63	44.96	4.03
Thorax mass (mg)	M	10.78	1.13	12.13	1.20	11.74	1.23
	F	12.34	1.27	13.53	1.44	12.28	1.67
Abdomen mass (mg)	M	11.22	2.32	10.80	2.91	11.10	2.22
	F	25.22	4.20	26.18	2.23	26.21	2.38
Wing area (mm^2)	M	209.27	18.44	224.80	19.16	218.14	18.70
	F	269.80	20.08	275.81	18.98	264.53	7.24
Aspect ratio (wing span^2/wing area)	M	3.61	0.16	3.49	0.20	3.55	0.23
	F	3.46	0.16	3.39	0.20	3.61	0.27
Wing loading (dry mass/wing area)	M	0.13	0.02	0.13	0.01	0.13	0.01
	F	0.16	0.01	0.17	0.01	0.17	0.02

M, male; F, female. For all variables except aspect ratio, males were significantly smaller than females ($p < 0.004$ in all cases). Only thorax mass was significantly different among regions, with individuals from East Sussex having significantly larger thoraxes than those from Surrey ($F_{2,50} = 5.14$, $p = 0.009$).

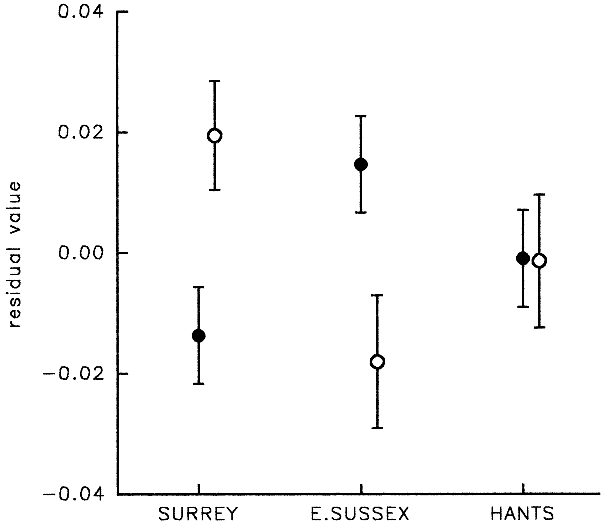

Fig. 2. Relative investment in thorax (●) and abdomen (○) (measured as residual of regression of log thorax mass or log abdomen mass on log total mass) in individuals from Surrey, East Sussex and Hampshire. Means and standard errors are shown.

sex and region as factors and colonisation/refuge nested within region; $F_{2,50}=1.27$, $p=0.29$) or between colonised and refuge sites ($F_{3,50}=0.44$, $p=0.72$). There was also no difference in relative thorax mass between colonised and refuge sites ($F_{3,50}=0.56$, $p=0.65$).

3.4. Relative investment in abdomen

The slopes of the relationships between total mass and abdomen mass did not differ significantly among regions (ANCOVA with sex and region as factors and total mass as a covariate; $F_{2,49}=1.77$, $p=0.18$) or between sexes ($F_{1,49}=2.42$, $p=0.13$). As above, residuals were calculated for each individual from regressions of abdomen mass on total mass (separate regressions for each sex). There were significant differences among regions in relative abdomen mass ($F_{2,50}=3.82$, $p=0.029$); individuals from East Sussex had relatively small abdomens and Surrey individuals had relatively large abdomens (Fig. 2). These differences corresponded to little difference in absolute abdomen mass (Table 2), but since these values do not take account of overall size, they should be treated with caution. As with relative thorax values, there was no difference in relative abdomen mass between colonised and refuge sites ($F_{3,50}=0.66$, $p=0.58$).

4. Discussion

4.1. Morphology in refuge and colonised sites

The distribution of *H. comma* along the North and South Downs in S.E. England contracted to its lowest levels during the 1970s and early 1980s, and *H. comma* currently occurs in only four regions in this area (Thomas and Jones, 1993). Over the past 20 years, however, there has been an increase in the distribution of *H. comma*, and its present distribution reflects the location of refuge areas, the distribution of currently suitable breeding habitats, and the ability of individuals to colonise habitats from refuges.

We found no differences in adult morphology between refuge and colonised sites within regions. This contrasts with other studies which have shown increased frequency of dispersal morphs in recently colonised habitat (Nielmela and Spence, 1991). In the present study, however, sampled sites varied in time-since-colonisation, which ranged from a minimum of 5 years to c. 20 years (generations). If colonising individuals had differed in their dispersal morphology (Nielmela and Spence, 1991), selection might have removed such differences during the time since colonisation (Roff, 1990). Alternatively, reverse gene flow from colonised sites to refuge sites, once colonised populations were large, may have changed traits in refuge sites. This effect would be expected to be greatest in East Sussex, where the ratio of refuge to colonised sites is lowest.

A third possibility is that selection was simply not strong enough to give rise to evolutionary changes during colonisation. Assuming patches were colonised from the nearest occupied patch rather than from the original refuge, colonisation distances differed among regions and were 3550 m in Hampshire, 225 m in East Sussex, and 600 and 220 m in Surrey (White Downs and Reigate Hill, respectively). Many individuals are likely to move several hundred metres (Hill et al., 1996), so colonisation bottlenecks may not have been particularly narrow. Thus, colonists may not necessarily have greater flight ability (Simberloff, 1981).

4.2. Habitat structure and flight morphology

There were significant differences in flight morphology among regions. Individuals from Surrey had relatively small thoraxes while individuals from East Sussex had relatively large thoraxes, with Hampshire individuals having intermediate values. In butterflies, thorax mass is principally flight muscle mass, and butterflies with large flight muscles, from East Sussex, would be expected to be faster fliers (Dempster et al., 1976; Srygley and Chai, 1990), and might therefore have greater dispersal potential (e.g. ability to fly further or increased tendency to disperse). However, there are currently no independent data on the relationship between flight morphology and mobility in *H. comma* and further studies are needed to clarify the biological implications of differences in body morphology on flight ability in this species.

Individuals with relatively large thoraxes necessarily also had relatively small abdomens because thorax mass plus abdomen mass comprised c. 70% of total mass. Thus individuals from Surrey had relatively large abdomens and individuals from East Sussex had relatively small abdomens. However, given that thorax and abdomen measures are not independent, it is impossible at this stage to separate the effects of selection on different body parts, or to determine where selection is acting. The subsequent discussion focuses on results from thorax data because they are more directly relevant to evolutionary changes in dispersal rates, but this does not exclude the possibility that selection is also acting on investment in reproduction.

Individuals in East Sussex had relatively large thoraxes and were associated with landscapes where habitat patches were further apart and colonisation distances were longer (Table 1), while in Surrey, individuals had relatively small thoraxes and occupied habitat patches that were closer together. In addition, distances between vacant and occupied sites were shorter in Surrey, suggesting that individuals were poorer colonisers, although vacant patches were also smaller in Surrey and therefore less likely to be found by colonisers (Thomas and Jones, 1993). These results suggest a relationship between morphology and the spatial distribution of habitat, with populations with relatively large thoraxes colonising landscapes where habitat patches are far apart.

In the absence of data to the contrary, we have assumed that differences in flight morphology are related to dispersal potential. However, flight has many functions in addition to long-distance dispersal (e.g. foraging, mate-location, predator-avoidance, finding oviposition sites) and there are many aspects to flight (speed, duration, agility, manoeuvrability, etc.). Different morphologies are advantageous for different types of flight (Betts and Wootton, 1988; Chai and Srygley, 1990; Srygley and Chai, 1990). It is possible, therefore, that results from this study may arise from effects of landscape pattern on selection for other flight-related behaviours than those directly related to dispersal in fragmented habitats (Wickman, 1992; Van Dyck et al., 1997).

4.3. Wider conservation implications

The apparent difficulty some species have in colonising suitable but unoccupied habitats (Thomas and Jones, 1993; Thomas et al., 1992) highlights the urgent need to understand factors affecting dispersal and colonisation in populations that inhabit modern landscapes. Although we compared only three metapopulations, results from this study suggest that evolutionary differences may be associated with populations that inhabit landscapes with different levels of fragmentation. Extinction and colonisation dynamics, as well as population isolation, may result in the rapid evolution of morphology in modified landscapes (Dempster et al., 1976; Dempster, 1991; Thomas et al., 1998). Such changes are clearly important for the survival of species. This study suggests that evolutionary differences in flight morphology may influence the ability of butterflies to colonise empty habitat patches scattered across fragmented landscapes. Predictions of where natural colonisation will or will not take place can thus depend on the specific evolutionary background of the source populations, as well as on the physical distance between remnant populations and potential, but empty habitat. This has clear practical implications in conservation management, such as where species (re)introductions will be required, and where to create stepping stone habitats to allow natural expansion of populations.

Evolutionary responses to habitat fragmentation are likely to differ among species and further comparative studies are required to assess whether recent evolutionary changes in dispersal rates are widespread responses to habitat fragmentation, and how frequently these changes need to be considered during the development of practical conservation programmes.

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