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ORIGINAL PAPER

Key traits in a threatened butterfly and its common sibling: implications for conservation

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Abstract We ask here which traits predispose one species to extreme rarity and possible extinction while a sympatric sibling is geographically widespread. With background knowledge on the level of habitat specialization of the two species, the population structure and movement of the localized and threatened *Orachrysops ariadne* were compared to those of the common and highly sympatric *O. subravus*, using mark-release-recapture. Of a total of 290 marked *O. ariadne* individuals 42.8% were recaptured, while of 631 *O. subravus* individuals 49.3% were recaptured. The Jolly-Seber model was used to estimate daily population numbers (N_i), survival rates (ϕ_i), recruitment rates (B_i), proportion of marked animals in the total population ($\propto_i$), and the number of marked animals at risk (M_i). *O. ariadne* is a remarkably rare animal, averaging only 10 individuals ha^{-1} within its small, remaining colonies. Average residence times of male adults were generally similar in both species, being just over 5 days. *O. ariadne* is a strong and rapid back and forth flier, covering mean recapture distances of 157 m, almost twice that of *O. subravus*, principally in search of scarce nectar sources. In short, the rarity of *O. ariadne* is not so much to do with behaviour, survivorship or longevity, but rather with limited availability of the specialized habitat patches for both larvae and adults, and, in particular, the extreme scarcity of the host plant. Evidence suggests that there has been very high selection pressure on the key trait of strong flight as a compensation for going down the apparently highly risky path of extreme microhabitat specialization. Of concern for conservation of this rare species is that these rare habitat patches have become increasingly isolated through transformation of the surrounding landscape. Reduction of the barrier effects of agroforestry through creation of linkages between colonies is recommended, especially as *O. ariadne* is such a strong flier. Such corridors are indeed now being implemented.

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Introduction

Some naturally rare species are geographically confined, simply because they have specialist resource requirements which are also scarce (Gaston 2003). For insects which are specialist endemics, this often means that they are confined to small-sized habitat patches. Insects in such patches are vulnerable to anthropogenic impact when that impact exactly coincides with their limited geographical range (Samways 2006). For example, afforestation of a landscape supporting a narrow-range endemic could be devastating for it. Yet conversely, a small natural patch can be set aside especially for that species. Such a small patch may be adequate, at least in the short term, for supporting the species, as appears to be the case for some lycaenids in South Africa (Lu and Samways 2001; Edge 2006).

Although considerable work has been done on the impacts of landscape fragmentation on butterflies, there is very little research on how traits of these narrow-range endemics vary in comparison with those of common species (Gaston 2003). This dearth of information is not surprising given that it is a difficult topic to investigate, owing to phylogenetic and geographical constraints. For such studies, it is essential to compare sibling species living in the same place. If these two variables are not addressed, there is a risk that traits will vary according to phylogeny as well as to spatially different environmental variables. These factors are built into this current study.

The Karkloof blue butterfly *Orachrysops ariadne* (Butler) is endemic to South Africa and is globally Red-listed as 'Vulnerable' (IUCN 2006). It is currently known from only four small and threatened sites. Arguably, it is on the verge of extinction. Three of these are within 30 km of each other, although still likely to be separate subpopulations. It is nevertheless conceivable that occasional individuals may move from one population to another (see Schmitt et al. 2006). The fourth site is over 100 km away. In contrast to *O. ariadne*, the sibling and highly sympatric species, the Grizzled blue butterfly *O. subravus* (Henning and Henning), is a common species, and is widespread from the Eastern Cape Province to the KwaZulu-Natal midlands (Pringle et al. 1994). These two species provided an opportunity for investigating how their mobilities and related traits differed. One would expect perhaps that the narrow-range endemic might have weaker flight, tighter turning circles, or other traits which have been selected for survival in size-restricted patches. Understanding traits of threatened species relative to common species, helps us make more informed decisions on their conservation (Shreeve 1995). Thus a further aim of this study was to determine which are the key traits to take into consideration for conservation of *O. ariadne*.

Study sites and methods

Sites

The farm Wahroonga (29°36′ S, 30°07′ E), which was selected for a mark-release-recapture (MRR), is a fine example of Mistbelt grassland (a high-elevation grassland often

Surrounding Wahroonga are pastures and timber plantations. *O. ariadne* inhabits about 10 ha of tall grassland on the southwest-facing slope, adjacent to pastures (Fig. 1). *O. subravus* inhabits a further 10 ha of shorter grassland on the north- and west-facing slopes, adjacent to timber plantations (Fig. 1). These two sites were separated by a strip of Mistbelt forest. The grassland/plantation boundary and a further side adjacent to buildings were burned every year as firebreaks. The rest of the grassland was burned on a rotational basis (2–4 years).

Study animals

Both *O. ariadne* and *O. subravus* are univoltine (one brood per year), but fly at different times of the year, March–April for *O. ariadne* and late August–November for *O. subravus*. Female *O. ariadne* uses the host plant *Indigofera woodii* H. Bol. var. *laxa* for oviposition and is ant-dependent, with the young larva being associated with *Camponotus natalensis* (F. Smith). Female *O. subravus* uses both *I. woodii* var. *woodii* and *I. tristis* E. May for oviposition. The life cycle of *O. subravus* is not fully known, but an ant, *Camponotus* sp., is associated with its larva. Further details of the life history and resource base used by *O. ariadne* are given in Lu and Samways (2001, 2002). Both species are strong fliers, with frequent changes of direction (Pringle et al. 1994).

Methods

The four extant colonies of *O. ariadne* vary in size from 1 to 10 ha. With the limitation of number of suitable sites for MRR of *O. ariadne*, it is not possible to undertake a study of the species as a large-scale, replicated experiment. Nevertheless, after initial appraisal of the largest site, Wahroonga, indications were that this large colony could sustain a

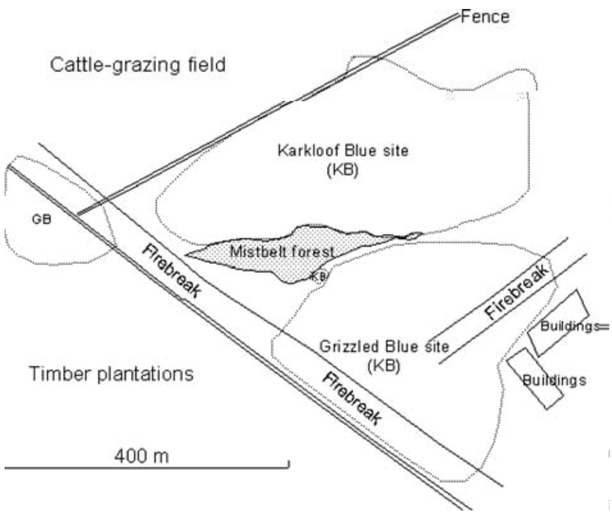

Fig. 1 Study site at the Wahroonga farm

carefully handled MRR study. *O. subravus* also occurred at the site, and this co-occurrence afforded the opportunity of comparing adults of the two species.

MRR has been widely employed to estimate absolute population parameters in mobile animals (Arnold 1983; Southwood and Henderson 2000). It estimates population size by using ratios of marked to unmarked individuals. This technique is also particularly useful for monitoring movements of butterflies (Scott 1975; Warren 1987; Wahlberg et al. 2002). In addition, it can also be used to estimate population structure, including composition by age and sex. As *O. ariadne* is a threatened species, the individuals were handled as softly as possible to reduce stress on them (Morton 1982; Murphy et al. 1986; Murphy 1988).

At Wahroonga in 1999, the flight season of *O. ariadne* was from 4 March to 22 April, and *O. subravus* from 6 September to 7 November 1999. During these times, a MRR study was undertaken to estimate each species' population size, sex ratio and adult movement patterns. Butterfly sampling was performed two to three times daily, as weather permitted. Each individual was caught, numbered on the hindwing using a permanent felt-tip pen, and immediately released. Recaptures indicated that marks were recognizable as long as the wings did not sustain any later, major damage.

The following data were recorded for each capture: number of mark, sex, time and position of capture. The degree of wing-wear was also recorded as follows: 0.5 = very fresh, 1.0 = fresh, 1.5 = fresh-intermediate, 2.0 = intermediate, 2.5 = intermediate-worn, 3.0 = worn and 3.5 = very worn (cf. Murphy et al. 1986). The Fisher-Ford, Manly-Parr and Jolly-Seber models are three of the most widely applied multiple-marking models. The Fisher-Ford method requires more assumptions but few data, while the Manly-Parr method needs few assumptions but requires the sampling of a relatively high proportion of the population (Southwood and Henderson 2000). On several days, the daily recapture rate was lower than the minimum proportion suggested by Manly-Parr. For this reason, we chose the Jolly-Seber stochastic model for estimation of population parameters (http://www.nhsbig.inhs.uiuc.edu/wes/populations.html).

Average residence rates (including losses due to emigration and deaths) were estimated from recapture decay plots. The total number of brood was estimated using the method of Watt et al. (1977), i.e., $\Sigma N_i(1 - \phi_i)$ the sum of daily population estimates was multiplied by the average daily lost-rate (1-average residence rate). Geographic information system (GIS) and a global positioning system (GPS) (accurate to 2 m) were used for mapping the position of each capture and recapture. Distances travelled (in metres) between each capture point were calculated as straight lines. The following mobility parameters were then calculated for each recaptured individual):

d_i : minimum distance in metres between capture i and $(i + 1)$;
t_i: time in days between capture i and $(i + 1)$;
D: sum of d_i's for each individual (minimum distance moved);
D_{max}: maximum D recorded in the population;
R: the distance in metres between the two farthest capture points (minimum range);
R_{max}: maximum range recorded within each population;
T: the number of days between first and last capture.

The sample size of d_i and t_i is total number of recaptures, and the sample size of D, R and T is the number of individuals recaptured (Scott 1975; Warren 1987).

Results

Capture sex ratio and butterfly physical condition

A total of 290 *O. ariadne* were marked over 48 days between March and April, and 124 (42.8%) were recaptured at least once. The overall sex ratio for *O. ariadne* was unequal, being 246 males and 44 females (5.6:1). Early in the flight season, the captures consisted almost entirely of males. In contrast, during the last few days of the flight period, only females were surviving and on the wing. The wing-wear rating of the newly marked individuals was mostly 'fresh' (47.2%) to 'fresh-intermediate' (19.7%), the remainder being old individuals.

Of 631 *O. subravus* marked between September and November, 311 (49.3%) were recaptured at least once. The overall sex ratio of *O. subravus* was 1.6:1 (387 males and 244 females). The sex ratios (male:female) of *O. subravus* in the early half of flight season were male biased, but female biased towards the end of the flight period. The wing-wear rating of the newly marked individuals was mostly 'fresh' (18.7%), 'fresh-intermediate' (31.1%) and 'intermediate' (31.2%), the remainder being old individuals.

Daily population size and total number of brood

Due to the low recapture rate of females (only four female individuals were recaptured) for *O. ariadne*, only males were used for the estimation of population parameters from Jolly-Seber model. The main flight season of *O. ariadne* was about 1 month, from mid-March to mid-April, when most of the adults (90%) were caught. Population estimates for males ranged from a low of 23 on 11 March to a high of 205 on 23 March, with an overall average population size of 92.3 (SD = 58.4). Population estimates when lumping both sexes together gave an overall average population size of 111 (SD = 68.5) individuals. The population peaked on 1 April and is consistent with the Jolly-Seber estimate of recruitment (B_i). Daily population size estimates for males had large standard errors owing to low recapture rate.

Daily population size estimates for *O. subravus* males were more reliable than those of females, as more males were captured. The main flight season of *O. subravus* was about two months, from early September to late October. Population estimates for males ranged from a high of 186 on 11 October to a low of 31 on 30 October, with an overall average population size of 82.9 (SD = 44.1) individuals. Female population size ranged from a high of 124 on 19 September to a low of 9 on 30 September, with an overall average population size of 60.4 (SD = 36.1) individuals. Population size estimates of both sexes together was 240.1 (SD = 226.6) individuals.

Total number of brood was estimated at 624 male *O. ariadne*. The female *O. ariadne* could not be calculated owing to the small number of recaptures. Total number of brood was estimated at 538 male and 424 female individuals of *O. subravus*.

Recapture probabilities and residence

O. ariadne showed a bias towards males over females captured, both as a sex ratio and as a substantially higher rate of recaptures per individuals. This contrasted with *O. subravus* where differences in sex ratio and in number of recaptures were considerably lower.

Recapture decay plots of male *O. ariadne* ($y = 5.44 - 0.299x$, $r^2 = 0.983$) (where y = recapture rate, and x = time), male *O. subravus* ($y = 5.364 - 0.244x$, $r^2 = 0.946$) and female *O. subravus* ($y = 4.09 - 0.226x$, $r^2 = 0.964$) showed that residence has a constant loss rate. Average residence times of adult males were very similar in both species in the range of 5.36–5.44 days, and were slightly longer for male than for female *O. subravus* (by 4.09 days). The maximum longevity observed was 18 days for male *O. ariadne*, 18 days for male *O. subravus* and 19 days for female *O. subravus*.

Adult movement pattern and parameters

The flight paths of male *O. ariadne* movement during the MRR study are shown in Fig. 2. The *O. ariadne* males patrolled widely back and forth within the whole colony (Fig. 2), where nectar sources are abundant. The presence of Mistbelt forest restricted the free movement of individuals. *O. ariadne* flew along the edge of the Mistbelt forest, and only crossed this barrier at narrow gaps at the end of the Mistbelt forest patch. Some of the male adults that were marked at the periphery of the colony were recaptured well within the colony where the host plant was abundant.

Examples of flight patterns of *O. subravus* are given in Figs. 3 and 4. Most of the adults flew within the colony, searching for host plants or nectar plants which were mainly along firebreaks where the nectar plants and host plants had recently emerged after fire. The firebreak, with its abundance of nectar plants, meant that *O. subravus* was frequently encountered. Furthermore, the *O. subravus* flight domain shifted according to the spatial appearance of nectar plants. The Mistbelt forest also restricted movement of *O. subravus* individuals, which flew only along the edge of the forest patch.

Adult movement parameters of *O. ariadne* and *O. subravus* are given in Tables 1 and 2. The maximum recorded movement range (R_{max}) of male *O. ariadne* on the same day was 310 m and over more than 1 day was 320 m, which is nearly the maximum length of the

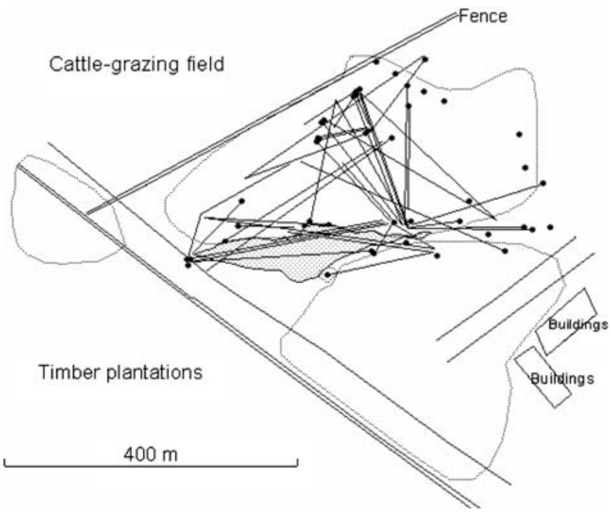

Fig. 2 Male *Orachrysops ariadne* movement at the site. Dots indicate points of initial capture and lines indicate each movement recorded

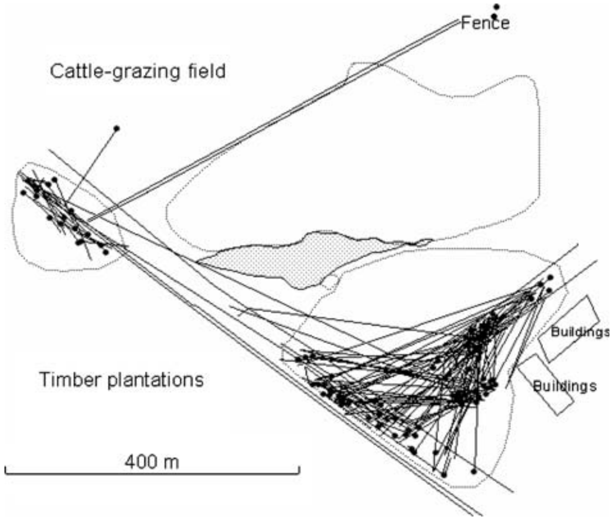

Fig. 3 Male *Orachrysops subravus* movement at the site. Dots indicate points of initial capture and lines indicate each movement recorded

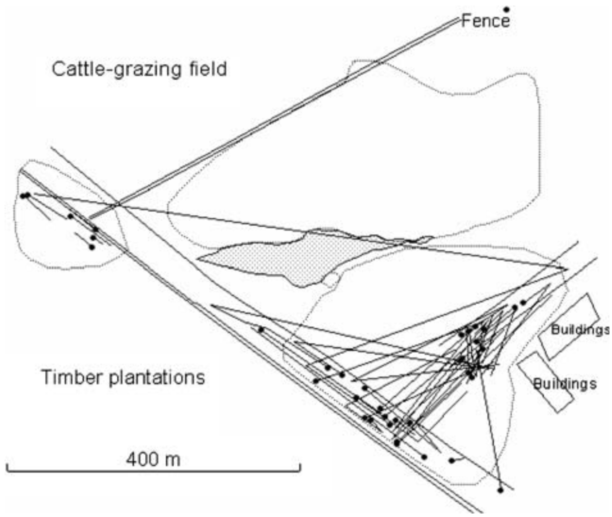

Fig. 4 Female *Orachrysops subravus* movement at the site. Dots indicate points of initial capture and lines indicate each movement recorded

site. The R_{max} of male and female *O. subravus* on the same day was 350 and 320 m, respectively, but over more than 1 day it reached 680 and 750 m, respectively. But the mean range (R) of *O. subravus* (102–104 m) was significantly smaller than that of *O. ariadne* (177 m) (t = 6.01, p < 0.0001). Although the vast majority of *O. subravus* individuals were recaptured within the colony, a few individuals (0.05%) were recaptured in neighbouring areas through additional sampling efforts.

Table 1 Adult Karkloof blue *Orachrysops ariadne* movement parameters when recorded over 1 day or more

Movement parameter	Males	Females
Number of individuals marked	246	44
Number of individuals recaptured	95	4
Total number of recaptures	148	5
Mean T (days)	5.67	5.25
Mean t_i (days)	3.69	4.2
R_{max} (m)	320	200
Mean R (m)	177	–
Mean D (m)	219	–
Max D (m)	780	–
Mean d_i	157	–

Table 2 Adult Grizzled blue *Orachrysops subravus* movement parameters when recorded over one day or more

Movement parameter	Males	Females
Number of individuals marked	387	244
Number of individuals recaptured	137	61
Total number of recaptures	212	80
Mean T (days)	5.26	4.05
Mean t_i (days)	3.51	3.34
R_{max} (m)	680	750
Mean R (m)	104	102
Mean D (m)	162	142
Max D (m)	1260	1300
Mean d_i	81	89

The mean flight distance (d_i) of male *O. ariadne* (157 m) was significantly greater than that of male *O. subravus* (81 m) ($t = 6.16$, $p < 0.0001$) and female *O. subravus* (89 m) ($t = 4.1$, $p < 0.0001$). The results indicate that *O. subravus* is more sedentary than *O. ariadne*. Although the minimum total movement distance (D) for male *O. ariadne* was 780 m, which is smaller than for male *O. subravus* (1,260 m) and for female *O. subravus* (1,300 m). This may be partially explained by the fact that *O. subravus* individuals were recaptured many times and thus appeared to have greater ranges and total distances than *O. ariadne* males which were recaptured infrequently (Gall 1984).

Discussion

Threatened species are often assumed to be short-lived, comparatively sedentary, host-plant specialists, low in mobility and often are rare or local endemics (Gall 1984; Murphy et al. 1986; Shreeve 1995). In fact, many butterflies are capable of travelling long distances, although their activities are often restricted to relatively small areas, with some specialist butterflies being more mobile than previously thought (Mousson et al. 1999; Schmitt et al. 2006). These points will be considered further here.

Flight season

The peak flight season of *Orachrysops ariadne* was from mid-March to mid-April, while that of *O. subravus* was from early September to late October. The timing of the flight period of *O. ariadne* is different from all other eight species in the genus, which are on wing from September to December (Pringle et al. 1994). It is not clear why this is the case, but may be associated with the fact that the host plant is a prostrate form (although there are no details in the literature of the form of the host plants of the other eight species). For *O. ariadne* in its particular localities, March–April is a time when rains are subsiding and inundation of low plants is less likely, yet it is also prior to regular early morning dews and winter grassland fires, all of which could damage eggs and young larvae. Although a common species may have a population of enough individuals for at least some to survive such conditions, this is not likely to be the case for a small, geographically confined population, which is at so much more risk of local extinction.

Traits, population size and density

Both *O. ariadne* and *O. subravus* are similar in having protandry, male-biased seasonal sex ratios (even late in the flight season), similar wing-wear rating progression, constant population loss rates, number of MRR handling times per butterfly individual, and similar longest recapture periods.

The results here suggest that the sex ratio in *O. ariadne* (5.6:1) is heavily in favour of males, but less so in the case of *O. subravus* (1.6:1). These ratios are likely to be biased, as males are blue and conspicuous, while females are brown and inconspicuous. Females are also cryptic and low flying, searching for host plants compared with the males' higher, patrolling flight, and thus more easily caught (Schtickzelle et al. 2002; Maes et al. 2004). It is possible too, that they fly less than males, although there is no evidence that this is the case here. The difference in sex ratio between the two species may also arise from the way the two species respond to vegetation structure. Female *O. ariadne* search for host plants among dense, tall vegetation, whereas female *O. subravus* occur in open, newly burned firebreaks. Thus, females of *O. subravus* are much more easily captured, so biasing sampling.

The overall average population size was similar for both male *O. ariadne* and male *O. subravus*, although population estimates of both sexes together, indicated that the overall average population size of *O. ariadne* was just under half that of *O. subravus*, despite the flight season being half a month longer for *O. subravus*. This again may have sampling bias between females of the two species.

Density of *O. ariadne* was about 20 individuals ha^{-1} during the peak flight season, with a whole flight-season average of only 10 ha^{-1}. This is a similar figure to that of another colony at The Start (1 ha in size) (Lu and Samways 2001). The current population size and density estimates of *O. ariadne* suggest that the population levels are probably too low to sustain any loss of individuals. In terms of long-term genetic viability, the size of the *O. ariadne* Wahroonga population (ca. 600 individuals) is only a marginally safe number, in an area of about 10 ha. Of even greater concern are the other two smaller sites, The Start and Stirling, each of which is only 1 ha. The population levels for these two, very small populations are cause for considerable concern in view of multiple impacts in and around the colonies. Indeed, in view of Schultz and Hammond's (2003) findings on another lycaenid, the future for this species looks very bleak, without even invoking issues of climate change.

Residency and dispersal

Results from recapture decay plots indicated that residence has a constant loss rate. It is not clear whether this population loss is due to death or to emigration (Warren 1987). The wing-wear figures show that most of the butterflies when first caught were in good condition. It is possible that only old adults emigrate, as Gall (1984) found for *Boloria acrocnema* (Nymphalidae), which enables egg dispersal to new sites after first having ensured that some eggs are laid at the home site when the individual was younger.

The average residence times were similar in both species, and agree with other results on lycaenid butterflies (Arnold 1983; Fischer et al. 1999; Scott 1975; Maes et al. 2004). The longest recapture period was 18 days for male *O. ariadne* and the same for male *O. subravus*, while it was 19 days for female *O. subravus*. This suggests that the life span of *O. ariadne* and *O. subravus* can be at least this long. Repeated mating was confirmed to occur in *O. subravus*, but whether this occurs in *O. ariadne* is uncertain as only two sightings of mating pairs were made. The relatively long life span of both species suggests that multiple matings are probably more frequent than field observations indicate. The Karner blue butterfly (*Lycaeides melissa samuelis*) has a long daily active period (09h00 to 18h00 or 19h00), but lives for only a few days (Schweitzer 1994). In contrast, the daily activities of *O. ariadne* (10h00 or 11h00 to 14h00 or 15h00) and *O. subravus* (09h00 or 10h00 to 15h00 or 16h00) are shorter, possibly increasing survivorship through being less exposed to predation and wing tearing. Interestingly, mean flight distance of males of *O. ariadne* was about twice that of *O. subravus*, although the minimum total movement distance of *O. ariadne* was a little over half that of *O. subravus*. Thus, the threatened *O. ariadne* is potentially a more powerful flier than *O. subravus* but nevertheless tends to remain in the patch.

Habitat and host plant specialization

The distribution of both the host plant and the nectar plants appear to be the two limiting factors for the distribution of both species, as in many butterflies elsewhere (Murphy et al. 1984; Schultz and Dlugosch 1999). In the case of the two species here, *O. ariadne* is a particularly rare species, and its only host plant *I. woodii* var. *laxa* is extremely rare (Lu and Samways 2002). In contrast, *O. subravus* is more abundant and widespread, and its host plant, both *I. woodii* var. *woodii* and *I. tristis* together have a fairly wide distribution (Lu and Samways 2001). This resource availability may explain why *O. ariadne* is rare, while *O. subravus* is common, as Dennis et al. (2004) have suggested for other species pairs. Rare species may utilize resources which themselves occur at lower abundances or restricted areas than do those resources used by common species. Also, rare species often utilize a narrower range of resources than do common species (Gaston 2003), as appears to be the case for these two species. Interestingly, Koh et al. (2004) have shown that specificity of larval host plant and adult habitat specialization are the best correlates of extinction risk for butterflies in Southeast Asia.

Host plants and dispersal

The host plant of the larva and nectar sources of the adult are uneven in distribution within the heterogeneous habitat. Thus, plant resource distribution is critical in determining the population spatial structure and movement in butterflies (Arnold 1983; Brommer and Fred 1999). The differences in the movement patterns and mean distances between *O. ariadne* (157 m) and *O. subravus* (81–89 m) are mainly explained in the distribution patterns of adult nectar plants and host plants. The more abundant and clumped distribution of nectar flowers for *O. subravus* results in more short-distance movements in and around nectar clumps, while *O. ariadne* flies longer distances in search of its scarce nectar flowers.

O. ariadne has a strong flight, back and forth within the colony. Furthermore, the life span is not as short as originally thought. These two factors make possible the opportunity for long-distance dispersal, but whether it occurs on a regular basis or not is not known. In summary, and to return to the opening sentence of this Discussion, *O. ariadne* is not short-lived, nor sedentary, nor with low mobility in comparison with its common, sympatric sibling. It is however, an extreme host plant (and hence habitat) specialialist, which in turn predisposes it to extinction risk.

Conservation management

As the results here illustrate that *O. subravus* flies beyond the core of the colony, based on the recapture decay plots, *O. ariadne* may also do so on a regular basis. The problem remains however, that for *O. ariadne*, it must find suitable or potential habitats with only about 1% of good quality Mistbelt grassland surviving anthropogenic attrition of the last two centuries (Lu and Samways 2002). Even if suitable vacant habitat patches exist, the species still has to cross considerable unsuitable habitat, particularly plantation forestry and crop fields. This is a serious problem because butterfly flight paths can be deflected by tall, alien trees (Wood and Samways 1991), and another lycaenid, the Adonis blue *Lysandra bellargus*, will not cross even 100 m gaps of agriculturally improved grassland (Thomas 1983). As with other butterflies, these results suggest that there needs to be better management of remaining fragments and better integration of the surrounding landscape between protected areas (Thomas 1995; Thomas and Hanski 1997; Warren 1993; Schmitt et al. 2006). Understanding the population structure and mobility of *O. ariadne* have become important dimensions for its conservation, especially in the highly fragmented landscape, as for *Lycaena helle* in Germany (Fischer et al. 1999). Conservation priorities in fragmented landscape may therefore require the establishment of network of suitable habitats (Baguette and Schtickzelle 2003; Mousson et al. 1999). Nevertheless, progress is being made, with habitat linkages being installed in this southern African landscape for butterflies and for other biodiversity (Pryke and Samways 2001, 2003), and which form a conservation network connecting the nodes occupied by colonies of *O. ariadne* (Samways 2007).

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