

Behavioural modes in butterflies: their implications for movement and searching behaviour

Article

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29 behaviour on movement predictions by comparing a mode-switching model with a version
30 including intraspecific variation and another assuming homogeneity between individuals. For
31 both sexes, including modes affected the mean and shape of the displacement rate compared
32 to models assuming homogeneity, although for females modes increased displacement 1.5
33 times while for males they decreased it by a third. Both models also differed substantially
34 from models assuming intraspecific variation. Finally, using a new model of search behaviour
35 we investigated the general conditions under which individuals should engage in an exclusive
36 search for host plants or receptive females. Parameterized for *M. jurtina*, the model predicted
37 males should engage exclusively in mate search, but females only when searching is very
38 efficient. The model provides a framework for analysing the searching behaviour of other
39 butterfly species.

40 **Keywords:** *Maniola jurtina*, meadow brown, motivation, movement

41

42 A fundamental aspect of the behaviour of an animal is the way it moves through its
43 environment. Movement is evaluated from several standpoints (sensu Tinbergen 1963)
44 varying from the mechanistic or biomechanical (e.g. animal locomotion; Alexander, 2003) to
45 considerations of adaptive purpose (e.g. optimality; Charnov, 1976). Current research in
46 movement ecology intersects these areas (Holyoak, Casagrandi, Nathan, Revilla, & Spiegel,
47 2008), linking the observed movement of individuals to the motivational states that underpin
48 them (Nathan et al., 2008). A key assumption of much recent modelling is that animals
49 switch between distinct movement patterns, often referred to as ‘modes’, as a result of the
50 local environment and their motivation (Fryxell et al., 2008; Morales & Ellner, 2002;
51 Morales, Haydon, Frair, Holsinger, & Fryxell, 2004; Skalski & Gilliam, 2003). Here modes
52 refer to temporally and spatially correlated movement patterns adapted to achieving a specific

53 goal (e.g. foraging). Identifying modes offers many benefits: first, it allows quantification of
54 the features of a behaviour (Jonsen, Myers, & James, 2006; Weimerskirch et al., 2002);
55 second, it links behaviours to the distribution of individuals across landscapes (Börger,
56 Dalziel, & Fryxell, 2008; Singh, Börger, Dettki, Bunnefeld, & Ericsson, 2012); and third, the
57 optimality of the movement patterns for their inferred purpose can be examined (Avgar,
58 Kuefler, & Fryxell, 2011; Dias, Granadeiro, & Palmeirim, 2009; Louzao, Wiegand,
59 Bartumeus, & Weimerskirch, 2014). However, linking movement modes with their
60 associated behaviours is challenging, as the accompanying behaviour is not always observed,
61 and internal motivations are hidden.

62 There has been a dramatic increase in the collection of movement data (Williams et al.,
63 2020), owing to remote technologies such as global positioning systems (GPS; Hebblewhite
64 & Haydon, 2010; Seidel, Dougherty, Carlson, & Getz, 2018). A challenge with these data is
65 that behaviours accompanying movements are not typically recorded. Behavioural modes,
66 therefore, must be inferred through statistical techniques (Patterson et al., 2017; Schick et al.,
67 2008), such as change point analysis (Killick and Eckley 2014) or state space modelling
68 (Patterson et al. 2008), that detect behavioural states in a time series of coordinates (Gurarie
69 et al. 2016). However, the method for tracking butterflies, a model group for the study of
70 movement and dispersal (Stevens, Trochet, Van Dyck, Clobert, & Baguette, 2012; Stevens,
71 Turlure, & Baguette, 2010), is unusual, as movements have often been recorded by directly
72 observing individuals over short timescales (Odendaal et al., 1989; Root & Kareiva, 1984;
73 Schultz, 1998; Schultz, Franco, & Crone, 2012; Turchin, 1991). An advantage of this
74 approach is that behaviours are recorded concurrently with movement data, and can be
75 categorized simply (Dover, 1989), generating contemporaneous movement and behavioural
76 information. This allows evaluation of the effect of observed behaviours on movement rates,
77 rather than inferring behaviour from movement data.

78 Previous studies have typically investigated movement modes in taxa larger and longer lived
79 than insects. In the Artiodactyla, movements transition broadly between encamped and
80 exploratory modes (Fryxell et al., 2008; Morales et al., 2004), further refined to bedding and
81 foraging (Franke, Caelli, & Hudson, 2004), predator avoidance (Forester et al., 2007) and
82 seasonal migration (Singh et al., 2012). Similarly, for pinnipeds, movement modes have been
83 identified for foraging at different depths (McClintock, London, Cameron, & Boveng, 2017),
84 in different seasons (Breed, Jonson, Myers, Bowen, & Leonard, 2009), and for engaging in
85 directed and undirected travel (Gurarie, Andrews, & Laidre, 2009). For butterflies, changes in
86 modes have often been associated with transitions between patches of varying habitat quality,
87 where movement rates change in response to resource densities (Fownes & Roland, 2002;
88 Odendaal et al., 1989; Ovaskainen, Luoto, et al., 2008; Schtickzelle, Joiris, Dyck, &
89 Baguette, 2007). Less explored is how butterfly movements vary within contiguous habitats
90 in response to motivation, and the consequences this has for movement rates and the fitness
91 of individuals.

92 It has long been recognized that butterflies engage in behavioural modes targeted at specific
93 purposes (Shreeve, 1992). Dennis and Hardy (2007) observed pierid species performing
94 foraging or directed flight patterns in response to habitat quality, and studies using harmonic
95 radar show butterflies engaging in distinct foraging or dispersive flights (Cant, Smith,
96 Reynolds, & Osborne, 2005). There is also much research on the sex-specific behaviours of
97 butterflies (Scott, 1974; Wiklund, 2003). For example, Brakefield (1982a) noted meadow
98 brown, *Maniola jurtina*, males engaging in patrolling behaviours, seeking out females on
99 sustained flights. Similarly in other satyrids, males are known to switch between territorial
100 and patrolling behaviours (Shreeve, 1984; Takeuchi, 2010; Wickman, 1985; Wiklund, 2003).
101 Thus, butterflies appear to perform distinct modes related to specific goals and these may be
102 consequential for understanding the movement of individuals and their distribution in an

103 environment. Including behavioural variation in models of butterfly movement is known to
104 affect predictions of movement rates (Evans et al., 2020b, 2020a); however, the way
105 behavioural differences are implemented may influence predictions. In many random-walk or
106 diffusion approaches individuals, at some level, are considered identical (Gurarie, Anderson,
107 & Zabel, 2009); thus, within a given habitat, movement observations may be pooled (Evans
108 et al., 2020b; Schultz & Crone, 2001). However, other approaches maintain behavioural
109 variation between individuals within the same habitat (Brown & Crone, 2016; Korösi,
110 Örvössy, Batáry, Kövér, & Peregovits, 2008). Not well considered thus far is the effect of
111 implementing behaviour through state switches, as has been applied in many other taxa
112 (Morales et al., 2004; Patterson et al., 2017).

113

114 Here we aimed to explore butterfly movement behaviour through identifying and describing
115 the behavioural modes of the model butterfly *M. jurtina*. To achieve this we utilized a large
116 data set of both movement and behaviour, collected within areas of varying habitat quality
117 (Evans, Sims, et al., 2019). Specifically, we aimed to (1) identify behavioural modes in the
118 sexes and between habitats of varying resource density, (2) quantify the movement
119 parameters associated with the modes, (3) demonstrate the consequences of behavioural
120 modes for the distribution of individuals across a landscape using an individual-based
121 random-walk model and (4) develop a model, from first principles, to explore the optimality
122 of exclusive search modes for reproductive resources. We focused especially on the effect of
123 behavioural modes in high-quality habitat as this is far less explored than the effects of
124 habitat quality on movement.

125

126 **<H1>Methods**

127 <H2>*Species*

128 *Maniola jurtina* is a common butterfly found throughout the British Isles and much of Europe
129 (Fox et al., 2015). It is a characteristic grassland specialist (Van Swaay et al., 2019), with
130 larvae feeding on common grasses and herbs (Ouin, Martin, & Burel, 2008) and the adults
131 obtaining nectar from a variety of flowers (Brakefield, 1982a; Dennis, 1992; Lebeau,
132 Wesselingh, & Van Dyck, 2017). The species is univoltine and typically on the wing between
133 June and September (Thomas 2010). The males emerge first (Brakefield, 1982b; Scali, 1971)
134 and are more active flyers than the females, spending extra time in flight searching for
135 receptive females (Brakefield, 1982a; Evans et al., 2020a; Evans, Sibly, et al., 2019a). The
136 females are monandrous and typically mate quickly after emergence (Dowdeswell, 1981).
137 When choosing host plants they are relatively unselective (Delattre et al., 2010), although
138 they show preferences for short grasses (Lebeau, Wesselingh, & Van Dyck, 2015). The adult
139 life span in the British Isles is 5–12 days although can be as long as 20 days (Brakefield,
140 1982b), with survival duration probably reflecting the amount and quality of nectar resources
141 (Evans, Sibly, et al., 2019b; Lebeau, Wesselingh, & Van Dyck, 2016a).

142

143 <H2>*Movement and behavioural data*

144 An open-access data set of butterfly movement was analysed (Evans, Sims, et al., 2019) and
145 as methods for this data collection are provided elsewhere we here provide only a brief
146 description. Butterflies were followed opportunistically with movement and behaviour
147 recorded simultaneously. Following a standard approach (Odendaal et al., 1989; Schultz,
148 1998; Turchin, 1991), movements were recorded by laying marker flags every time the
149 butterfly alighted or every 15 s during continuous flight. Observations ceased after 10 min or
150 after either 15 or 20 flags had been laid (15 flags in 2018 and 20 in 2017). The coordinates of

151 the flags were then retroactively mapped using a high-grade global navigation satellite system
152 receiver (Arrow 200 RTK GNSS, Eos Positioning Systems, Inc., Terrebonne, QC, Canada).
153 During the observations, behaviours were recorded continuously by categorizing behaviour
154 into flying, nectaring (taking nectar from flowers), basking (open wings and stationary),
155 inactive (closed wing and stationary) or ovipositing (Dover 1989). Timing of behaviour was
156 recorded accurately using a bespoke android phone app developed for the project.

157 Observations were relatively balanced between the sexes (184 ♀, 242 ♂), with most
158 observations taking place in nectar-rich habitats (rich: 321; poor: 105). Data on individual
159 flight tracks were collected over 72 days during the summers of 2016 (July–August), 2017
160 (June–September) and 2018 (June–July), at four sites in the south of England: North Farm in
161 Oxfordshire (51°37'N, 1°09'W), Jealott's Hill Farm, Berkshire (51°27'N, 0°44'W), the
162 University of Reading (51.4414° N, 0.9418° W) and Sonning Farm, Berkshire (51°28'N,
163 0°53'W). Three of the sites were agricultural farms that had implemented agri-environment
164 schemes and consisted of a mixture of arable fields, open meadows and nectar-rich field
165 margins, while the fourth consisted of areas of meadow within the grounds of the University
166 of Reading campus. Data were labelled dichotomously as either nectar rich or nectar poor,
167 with nectar-rich areas consisting of grasslands with a variety of wildflowers while the nectar-
168 poor sites were mowed grass with very few flowers. Hourly air temperature was collected
169 from local meteorological stations and mean solar radiation during observations (recorded
170 every 10 s) from dataloggers (HOBO pendant, Tempro Instrumentation, Arundel, U.K.).

171

172 <H2>*Ethical note*

173 Permissions were obtained from landowners for all sites visited during observations (The
174 Earth Trust, Syngenta Jealotts Hill, the University of Reading, Sonning Farm University of

175 Reading). All observations took place in the field and no butterflies were handled. The
176 methods applied for observing butterfly movement have been demonstrated to have no
177 observable impact on behaviour (Root & Kareiva, 1984)

178

179 <H2>*Statistical analysis*

180 To identify behavioural modes, the analysis was conducted in two stages. First, data were
181 collated into time budgets and a clustering approach was applied to group butterflies
182 performing similar behaviours across an entire observation. This we consider as
183 representative of a behavioural ‘mode’. In this first stage, observations from both sexes and
184 all habitat types were pooled and sex and habitat were used as predictors of cluster group
185 identity in a multinomial regression. This first stage identified that, as expected, sex and
186 habitat strongly predicted cluster grouping (see Results). Consequently, in the second stage,
187 observations were split by sex and habitat type and a separate cluster analysis was performed
188 to evaluate groupings in each sex*habitat combination. Identifying clusters in the nectar-poor
189 habitat allowed us to compare responses to habitat quality with those found in the literature,
190 although our analysis primarily focused on the modes of butterflies within nectar-rich
191 habitats.

192 Silhouettes (Rousseeuw, 1987) were used to identify the number of clusters, ranking the
193 proposed number by comparing the distances of objects contained within a cluster to the
194 distance of the nearest neighbour of an adjacent cluster. Implementations are available in the
195 R package ‘cluster’ (Maechler, Rousseeuw, Struyf, Hubert, & Hornik, 2019). This provided
196 an objective method to select the number of behavioural clusters in the data. With the number
197 of cluster groupings selected, *K*-means clustering (Hartigan & Wong, 1979) was applied. For
198 comparisons in stage 1, air temperature was introduced as a covariate, as insolation data were

199 unavailable in nectar-poor regions. For stage 2, however, within the nectar-rich habitat,
200 insolation was found to be a far superior predictor of clustering than air temperature (lower
201 Akaike information criterion) and was used instead.

202 To compare step distances and turning angles between clusters within nectar-rich habitats,
203 Tukey's test for comparing individual means was used for the step distances (Tukey, 1949).
204 Wallraff rank sum tests of angular distance were used to compare differences in turning
205 angles. Step distances were log transformed to meet the assumptions of Tukey's test.

206 Multinomial regression was carried out using the package 'nnet' (Ripley, Venables, &
207 Ripley, 2016), Silhouettes were produced using 'factoextra' (Kassambara & Mundt, 2017),
208 and Wallraff rank sum tests using 'circular' (Agostinelli & Lund, 2017) all within R 3.6.1 (R
209 Core Team, 2019).

210

211 <H2>*Random-walk models*

212 To explore the effect of behavioural modes on movement rates and the distribution of
213 individuals, a simple individual-based random-walk model was developed. The model
214 predicted the daily displacement from a fixed starting point after 8 h (28 800 s) of simulated
215 time. Three versions were produced; all were sex specific but differed in their treatment of
216 behaviour. The 'pooled' model simulated behaviour without reference to any behavioural
217 variation; this we considered typical of random-walk or diffusion approaches where
218 individuals are considered identical (Gurarie, Anderson, et al., 2009) and observations within
219 a habitat type often pooled (Evans et al., 2020b; Schultz & Crone, 2001). The 'mode' version
220 was a state switch model (Morales et al., 2004; Patterson et al., 2017) that included
221 transitions between modes and variation in step distances, turning angles and the proportion
222 of time in flight for the behavioural modes. Finally, in the 'intraspecific' model, variation

223 between individuals in movement propensity is seen as a fixed trait (Korösi et al., 2008) and
224 the amount of time in flight matched the proportions observed. The models contain variation
225 from different sources, the ‘pooled’ model from stochasticity in steps and turns, the ‘mode’
226 model additional stochasticity in choice of behavioural mode and the ‘intraspecific’ model
227 fixed individual variation in flight propensity.

228 In the pooled model, butterflies moved by selecting steps and turning angles from all data in
229 nectar-rich habitats. Movement occurred for a ‘flight time’ which was the mean of the
230 observed proportion of time in flight multiplied by the total simulated time. For example, if
231 butterflies spent on average 20% of their time in flight then total simulated flight time would
232 be $0.2 \times 28\,800 \text{ s} = 5760 \text{ s}$. For every step, the mean duration of the step distances was
233 subtracted, and movement stopped when all butterflies had run out of flight time. For the
234 mode model, butterflies selected behavioural modes in proportion to those observed in the
235 data. Each mode had a cluster-specific step distance distribution, turning angle distribution
236 and flight time (Tables S1 and S2). To match the timescale of the data collection, modes
237 switched every 10 min of simulated time, with the frequency of each mode proportional to
238 that observed in the data. The flight time in each of the 10 min was the average proportion of
239 time in flight for that cluster multiplied by 600 s and this was repeated until the total
240 simulated time had elapsed. In the intraspecific model, butterflies drew the proportion of time
241 in flight from observations but moved using pooled steps and turning angles. The pooling at
242 this stage was used because not all butterflies had sufficient steps to generate appropriate
243 individual turning angle and step distributions.

244 To compare the models, for each sex and model type combination, 5000 butterflies were
245 initialized at the centre of a 2 x 2 km landscape and the model was run for the simulated day.
246 The landscape was made sufficiently large to avoid any edge effects. At the end of the run
247 Euclidean distance from the start location for each butterfly was then recorded, thus

248 representing the total displacement and the change in the distribution of the butterflies in the
249 habitat.

250 The model was built in NetLogoR (Bauduin, McIntire, & Chubaty, 2019), a recently
251 developed set of individual-based functions inspired by the NetLogo language which can be
252 used for developing individual-based models within R (code is available at DOI:
253 10.17632/mm2skm8f6j.1). Turning angles were simulated used the ‘circular’ package
254 (Agostinelli & Lund, 2017).

255 <H2>*Exclusive search model*

256 A model was derived from first principles to explore the utility of searching behavioural
257 modes for both sexes. The model conceptualized a trade-off between exclusively searching
258 for the resources associated with reproductive fitness (e.g. host plants, receptive females) and
259 finding these resources as a by-product of normal, lower net-energy expenditure, behaviours
260 of foraging and inactivity. Specifically, the model aimed to explore how much time
261 individuals should dedicate to an exclusive search mode given (1) the change in resource over
262 time, (2) the energetic cost of search behaviour and (3) the relative effectiveness of exclusive
263 search over normal behaviours. It is assumed that when in exclusive search mode butterflies
264 trade life span for resources by consuming no nectar and thus use reserves, resulting in
265 reduced life span (Evans, Sibly, et al., 2019b; Lebeau et al., 2016a; Vande Velde & Van
266 Dyck, 2013). It is also assumed that butterflies can maintain net energy balance in
267 inactive/foraging modes by replenishing expended energy with nectar sugar and becoming
268 inactive to reduce metabolic rate (Lebeau, Wesselingh, & Van Dyck, 2016b; Niitepold, 2010;
269 Niven & Scharlemann, 2005). Thus, lifetime energy use can be represented as:

$$270 \quad L_e = E_s T_s$$

271 where L_e = lifetime net energy use, E_s = energetic cost of search (J/s), T_s = time in search (s)

272 This can be converted to a reduction in survival time by multiplying by a factor, A , that
273 relates energy loss to survival time. Combining E_s and A creates variable A' and the equation
274 for predicting life span is:

$$275 \quad LS = LS_n - A'T_s$$

276 where LS = life span (s) and LS_n = maximal life span (s).

277 Dividing this equation by the maximal life span generalizes the equation to different maximal
278 life spans and transforms times in modes into proportions of life span

$$279 \quad LS_p = 1 - A'T_{sp} \quad (1)$$

280 where LS_p = life span, T_{sp} = proportion of life span spent in search. Now A' is the amount by
281 which life span is reduced when the adult butterfly takes in no nectar.

282 Next, the proportional number of resources discovered during a lifetime is the sum of the
283 relative success of the two modes multiplied by the number of resources. First, the
284 approximate number of resources located is represented as

$$285 \quad \text{Area} \sim (1 - T_{sp}) + (T_{sp}B) \quad (2)$$

286 where Area = the area searched and B = the relative efficiency of search, or similarly stated,
287 the relative amount of area covered by exclusive search compared to nonexclusive search.

288 Resources are assumed to be uniformly spaced and so the number of resources located is the
289 product of the area searched (Area) and the density of resources. For replicating finite
290 resources, resources change through time using a linear function and so the density of
291 resources across a lifetime is the integral of the resource amount function multiplied by
292 equation (2). As either death of the butterfly or the total extinguishing of resources may come
293 first then the equations given below follow:

294
$$LS_p < \frac{1}{c} \rightarrow \int_0^{LS_p} 1 - ct \, dt = LS_p - c \frac{LS_p^2}{2} \quad (3a)$$

295
$$\frac{1}{c} < LS_p \rightarrow \int_0^{\frac{1}{c}} 1 - ct \, dt = \frac{1}{c} - \frac{1}{2c} \quad (3b)$$

296 where c = the rate of diminishment of resources over time and $1/c$ the point at which resource
 297 densities are 0.

298 Multiplying (3a) and (3b) by (2) produces equations for the relative number of resources,
 299 N_{items} , located during a lifetime, which can be evaluated in response to A' , B and c , the cost of
 300 exclusive search, its relative effectiveness and the rate of resource diminishment,
 301 respectively.

302
$$LS_p < \frac{1}{c} \rightarrow N_{\text{items}} = 1 - A'T_{sp} - c \frac{(1-A'T_{sp})^2}{2} ((1 - T_{sp}) + T_{sp}B) \quad (4a)$$

303
$$\frac{1}{c} < LS_p \rightarrow N_{\text{items}} = (\frac{1}{c} - \frac{1}{2c}) ((1 - T_{sp}) + T_{sp}B) \quad (4b)$$

304 For the analysis A' was estimated at 0.5 for *M. jurtina*, predicting a loss of 50% of life span
 305 when consuming no resources (Evans, Sibly, et al., 2019b; Lebeau et al., 2016a; Vande Velde
 306 & Van Dyck, 2013). The effects of variables B and c were then evaluated to determine how
 307 much exclusive search individuals should undertake to maximize the number of resources
 308 encountered. Presented results include evaluating T_{sp} after conditioning on c for values of 0
 309 and 1, relating to conditions where resources do not diminish (females locating host plants),
 310 and when resources are at 0 at 100% of total life span (assuming male life span is adapted to
 311 available reproductive opportunities).

312

313 **<H1>Results**

314 **<H2>Cluster analysis across habitat types and sexes**

315 Four clusters were selected by silhouettes of the time budget data, and *K*-means clustering
316 with four centres explained 80.8% of the variance in time budgets. The probability of an
317 individual being included in a particular cluster grouping was strongly predicted by sex and
318 habitat type (Table 1). Clusters consisted of four main groupings: (1) a combination of
319 basking, inactivity and flying that was shared in equal proportions between the sexes; (2)
320 large amounts of time in flight, the majority male, and located predominantly in nectar-poor
321 habitats; (3) inactivity, which was mainly female and split equally between habitat types; and
322 (4) nectaring, containing a higher proportion of females and found exclusively in nectar-rich
323 habitats. For convenience, we use the descriptive labels ‘high-bask’, ‘high-flight’, ‘high-
324 inactive’ and ‘high-nectar’, respectively.

325 Males had an increased probability of classification in the ‘high-flight’ cluster and a reduced
326 probability of classification in the ‘high-nectar’ cluster compared to females. In nectar-rich
327 habitats, ‘high-flight’ was reduced relative to ‘high-inactive’, meaning ‘high-flight’ was more
328 likely in nectar-poor habitats. The probability of being grouped into ‘high-bask’ also
329 increased in nectar-rich habitats. In contrast, there was no significant effect of habitat on the
330 probability of classification of ‘high-nectar’ relative to ‘high-inactive’. This may appear
331 counterintuitive, but it is due to the baseline condition of ‘high-inactive’ being common in
332 nectar-rich patches (Fig. 1).

333

334 <H2>*Clusters within sexes and habitat types*

335 When data were split by sex and habitat, different clusters were identified, with three groups
336 for females in nectar-rich habitat: (1) ‘high-nectar’; (2) ‘high-inactive’; and (3) ‘high-bask’ a
337 group that also contained inactivity, flying and oviposition. Male behaviour was more
338 diversified with five groups identified: (4) ‘high-flight’; (5) ‘high-nectar’; (6) ‘high-inactive’;

339 (7) ‘high-bask’ a group similar to that identified in females that contained basking and small
340 amounts of the other behaviours; and (8) an additional group containing a majority of
341 switches between inactivity and flight, termed here ‘mixture’. Males and females had similar
342 behavioural groupings in nectar-poor habitats, consisting of either ‘high-flight’ or ‘high-
343 inactivity’. For both sexes in nectar-rich habitats, insolation strongly influenced cluster
344 allocation (Table 2). In nectar-poor habitat, behaviour for both sexes was less diverse with
345 only two cluster groupings identified corresponding with a ‘high-flight’ and ‘high-inactive’
346 group.

347

348 <H2>Movement behaviour in sex-specific clusters

349 In nectar-rich habitats, step distances were found to differ between the clusters for both males
350 ($F_4=7.86$, $P<0.001$) and females ($F_2=4.97$, $P<0.001$). For males, Tukey’s test showed
351 differences mostly between ‘high-nectar’ and the other groups (‘high-inactive’, ‘mixed’ and
352 ‘high-flight’) with steps shorter for ‘high-nectar’ (Fig. 2a). ‘High-flight’ and ‘mixed’ were
353 also significantly different. Males’ turning angles varied between ‘high-nectar’ and all other
354 groups, with turning angles more tortuous in ‘high-nectar’ (Fig. 2b). There were also
355 differences between ‘high-flight’ and ‘high-bask’, and ‘high-bask’ and ‘mixed’ (full results
356 Table S3 and S4). For females, step distances were only significantly different between
357 ‘high-nectar’ and ‘high-inactive’ (Fig. 2c). There were also differences in turning angle
358 between ‘high-nectar’ and all other groups (Fig. 2d).

359

360 <H2>Consequences of behaviour modes for movement rates

361 The individual-based random-walk model was used to evaluate the effect of implementation
362 of behavioural differences on predicted movement rates within nectar-rich habitats. For both

363 males and females, the inclusion of modes and intraspecific variation had a large effect on the
364 mean and shape of the resultant displacement distribution (Fig. 3). Overall, the mode and
365 intraspecific models produced longer-tailed distributions than the pooled model, although the
366 models differed between the sexes. For males, the mean displacement of the mode model was
367 lowest (201 ± 1 m) followed by the intraspecific (239 ± 3 m) and then the pooled model (302
368 ± 1 m; Fig. 3a). However, the reverse was the case for the females where the mode model had
369 the largest mean displacement (106 ± 1 m), the intraspecific model was intermediate (101 ± 2
370 m) and the pooled model the lowest (70 ± 1 m; Fig. 3b).

371

372

373 <H2>Modelling optimal time in exclusive search

374 The optimal amount of time in exclusive search mode (T_{sp}) is shown against the efficiency of
375 exclusive search (B) and the rate of resource diminishment (c) in Fig. 4a. In general, when
376 efficiency is low and resources only slowly diminish, butterflies should spend little or no time
377 in exclusive search and should locate sex-specific resources as a by-product of behaviour that
378 maximizes survival. However, if resources diminish very quickly and exclusive search is
379 efficient, butterflies should spend all their time in exclusive search with a subsequent
380 sacrifice of life span. With no resource diminishment (Fig. 4b), a case likely to be
381 representative of *M. jurtina* which feeds on common grasses, females should only spend time
382 in exclusive search when its efficiency is 1.5 times that of survival/foraging behaviour. With
383 a higher rate of resource diminishment (Fig. 4c), a case representative of male *M. jurtina*
384 locating receptive females in this monandrous species, butterflies should always spend some
385 time in exclusive search even if it is only marginally more efficient than normal behaviour,
386 increasing up to more than 75% when search is twice as efficient.

387

388 <H1>Discussion

389 In this study, we explored various aspects of the behavioural modes of the model butterfly *M.*
390 *jurtina*. In nectar-poor regions, both sexes were characterized by modes of either inactivity or
391 high amounts of time in flight. In nectar-rich habitats, however, sex-specific behaviour was
392 more diversified. Females had three modes, ‘high inactivity’, ‘high-basking’ and ‘high-
393 nectar’, and males additionally had ‘high-flight’ and ‘mixed’ modes consisting of a high
394 proportion of time in flight, and transitions between flight and inactivity. Movement
395 parameters differed between the modes (Fig. 2) and their inclusion in a random-walk model
396 had large effects on the shape of the displacement distribution (Fig. 3). Including modes also
397 had different effects on the spatial distribution of the sexes, with males moving less on
398 average compared to the other model versions while for females including modes increased
399 movement. Finally, the model of exclusive search behaviour demonstrated the general
400 conditions under which exclusive search is favoured (Fig. 4) and indicated the time that
401 should be spent in exclusive search given its cost, its effectiveness and the rate of resource
402 diminishment.

403 In nectar-poor regions, behavioural modes were similar for the sexes, and consisted of either
404 inactivity or spending a high proportion of their time in flight. As these areas have low
405 resource densities, a parsimonious explanation for these modes is that flight and inactivity are
406 the only possibilities, thus requiring no account of motivation. However, as increasing
407 movement rate in response to poor-quality habitats is common to many butterfly species
408 (Fownes & Roland, 2002; Odendaal et al., 1989; Ovaskainen, Rekola, Meyke, & Arjas, 2008;
409 Roland, Keyghobadi, & Fownes, 2000; Schtickzelle et al., 2007; Zalucki & Kitching, 1982),
410 and is a general response across many taxa (Fryxell et al., 2008; Haskell, 1997; Smith, 1974;

411 Zollner & Lima, 2005), the ‘high-flight’ mode observed is likely to be a specific behaviour
412 pattern aimed at quickly moving *M. jurtina* out of poor-quality areas and not only a by-
413 product of low resource density. That movement in these areas is also faster and straighter
414 (Evans et al., 2020b) suggests that a ‘high-flight’ mode may correspond with exploratory or
415 dispersive movement (Delattre et al., 2010), as seen in many other taxa (Patterson, Thomas,
416 Wilcox, Ovaskainen, & Matthiopoulos, 2008) and is probably distinct from behaviour
417 occurring in nectar-rich habitats. This is most notable in the females where, in nectar-rich
418 habitats, the ‘high-flight’ mode was absent. Therefore, it seems likely that butterflies in
419 poorer-quality regions are either unable to fly due to thermal or physiological constraints, or
420 switching to flying frequently.

421 In nectar-rich habitats, males and females had different modes that largely corresponded with
422 previous work evaluating sex-specific behaviour in butterflies (Brakefield, 1982a; Scott,
423 1974; Shreeve, 1992; Wiklund, 2003). Females were either inactive, basking or nectaring.
424 This low-energy regime corresponds with maximizing adult life span which, from the
425 exclusive search model, is an optimal strategy. Females of *M. jurtina* progressively mature
426 eggs through their life span (Scali, 1971), probably producing a strong correspondence
427 between fitness and survival time. Oviposition was seen in the ‘high-bask’ cluster, although
428 still observed rarely. Therefore, it was not possible to determine a distinct oviposition mode.
429 Females of *M. jurtina* have a flight pattern that does correspond with oviposition, flying low
430 over the ground and laying a series of single eggs each a short distance apart, although this
431 was indistinct from other behavioural modes probably because of the timescale of our
432 observations. Males had two additional behaviours, ‘high-flight’ and ‘mixed’. ‘High-flight’
433 we consider to correspond with a behaviour termed patrolling (Brakefield, 1982a) where
434 males fly for longer periods as they search for receptive females and engage less in
435 behaviours such as nectaring and inactivity. The exclusive search model suggests this is an

436 optimal strategy for maximizing the number of receptive females located, incentivizing some
437 sacrifice of life span. The other mode termed ‘mixed’ may relate to perching behaviour seen
438 in the grassland species *Coenonympha pamphilus* (Wickman, 1985) and *Lasiommata megera*
439 (Dennis, 1982), the woodland species *Pararge aegeria* (Bergman et al., 2007; Shreeve, 1984;
440 Wiklund, 2003) and also possibly *M. jurtina* (Brakefield, 1982a). This is an alternative mate-
441 finding strategy where males wait inactive and chase females as they pass by. However, it is
442 also possible that, as butterflies were followed opportunistically, the ‘mixed’ mode consisted
443 of transitions between the other modes, rather than a specific behavioural pattern; therefore,
444 we limit our interpretation at this time.

445 For both sexes, movement parameters were found to differ largely between ‘high-nectar’ and
446 the other modes, although ‘high-flight’ also differed for males (Fig. 2). The short step
447 distances and tortuosity of ‘high-nectar’ are probably a by-product of moving from flower to
448 flower and slower flight speeds may relate to the ability to survey potential resources in flight
449 (Chittka, Dyer, Bock, & Dornhaus, 2003; Chittka, Skorupski, & Raine, 2009). ‘High-flight’
450 also probably results in longer step distances and straighter flight paths as males attempt to
451 survey larger areas when searching for females. The variation in the movement parameters
452 and the effect of implementing behaviour in the individual-based random-walk model
453 combined to have large effects on displacement distributions (Fig. 3). The relationship of the
454 mode model to the intraspecific and pooled models was qualitatively different between the
455 sexes. We attribute this to the mode model replicating transition through behavioural states,
456 generating females that move more than was observed individually (intraspecific model),
457 while also switching between the more and less diffusive movement states absent in the
458 pooled model. For males, the mode model was intermediate between the intraspecific model,
459 where observed individual differences are extrapolated, to the pooled model where
460 individuals are identical. Disentangling the effects of intraspecific variation versus

461 behavioural modes is challenging. Models that incorporate intraspecific variation in
462 movement rate have been successful in replicating realistic movement patterns (Brown &
463 Crone, 2016; Walters, Hassall, Telfer, Hewitt, & Palutikof, 2006) and there is good evidence
464 that traits such as metabolic rate consistently influence interindividual variation in movement
465 (Mattila, 2015; Ovaskainen, Smith, et al., 2008). Consequently, both movement modes and
466 syndromes (Sih, Bell, & Johnson, 2004; Spiegel, Leu, Bull, & Sih, 2017) are likely to be
467 important for understanding species movement rates. We suggest though, that for short
468 timescale observations (tens of minutes), such as those for butterflies, it may be challenging
469 to separate movement modes from individual propensities and their effect on movement
470 predictions needs careful consideration.

471 The exclusive search model provides the general conditions (Fig. 4) under which exclusive
472 search is favoured. In two examples, we considered nondiminishing and diminishing
473 resources, representing female *M. jurtina* searching for host plants and males searching for
474 receptive females. For females, exclusive search was only advantageous when it was more
475 than 1.5 times more successful for locating host plants than normal behaviour. As grasses are
476 relatively ubiquitous, females of *M. jurtina* can be predicted to have little exclusive search
477 behaviour and no specific mode for host plant search was in evidence. Similarly, as females
478 are monandrous, we expected males to engage in exclusive search and we found evidence of
479 patrolling behaviour. Generally, the amount of exclusive search could relate not only to
480 properties of flight paths but also to the distribution of resources. For example, pierid species
481 lay eggs on brassicas (Thomas, 2010) which are rarer and more clumped than grasses,
482 probably requiring an exclusive search for locating plants, and female pierids engage in
483 active search for host plants (Dennis & Hardy, 2007; Root & Kareiva, 1984). Likewise, in
484 polygamous species, or those with active females, we may assume less necessity for the
485 males to engage in exclusive search. Thus the model provides a framework to view the sex-

486 specific behaviour of many butterfly species from estimated parameters such as the cost of
487 search (widely available e.g. Lebeau et al., 2016b; Nütepöld & Boggs, 2015; Woods, Wood,
488 Ebersole, & Stevenson, 2010), the effectiveness of search and the rate of resource
489 diminishment. Some factors are not taken into account by the model, such as the effect of
490 different tactics used by perching or lekking butterflies (Alcock, 1985; Brown & Alcock,
491 1990; Scott, 1974), which would strongly influence both the success and the cost of search
492 (Dennis & Shreeve, 1988), although the model could be adapted through the appropriate
493 parameterization. Further, the assumption of uniform resources over the landscape is
494 simplistic, and it would be useful to evaluate how changes in the efficiency of search over
495 time might influence the use of exclusive search.

496 A limitation of this study is that the description of modes is related to the duration of
497 observations, risking the methods influencing our interpretation of the results. We feel here
498 though that the ability to group behaviour into meaningful clusters that correspond with
499 previous observations of butterfly behaviours demonstrates timescales at tens of minutes are
500 appropriate. Further, an ability to separate intraspecific variation from behavioural modes
501 would be enhanced by following butterflies for longer periods and attempting to observe
502 switches between modes within individuals. This is feasible, but due to the intensive nature of
503 the data collection would be time consuming to accumulate for a large sample of individuals.
504 Finally, the main focus of the study was behaviour operating within nectar-rich habitats, and
505 extrapolating movement to complex habitats will require a better understanding of how
506 modes change in response to habitat types, varying resource densities, habitat edges and an
507 individual's age and condition (Conradt, Bodsworth, Roper, & Thomas, 2000; Conradt &
508 Roper, 2006; Delattre et al., 2010; Kallioniemi, Zannese, Tinker, & Franco, 2014; Mair,
509 Thomas, Franco, & Hill, 2015; Polic, Fiedler, Nell, & Grill, 2014; Schneider, 2003). These
510 other factors may be particularly important for sedentary species like *M. jurtina* for which

511 mark–recapture studies find lower mean dispersal estimates (45–414 m; Schneider, Dover, &
512 Fry, 2003) than would be expected from direct extrapolations of movement observations.

513 In conclusion, we have identified the importance of behavioural modes for the fitness and
514 movement behaviour of the model species *M. jurtina*. Our results provide two main
515 innovations. First, we evaluated, in a movement model, the effect of behavioural modes on
516 predicted movement rates. Second, we produced a search model that conceptualized the
517 trade-off between searching for the resources necessary for reproductive fitness and searching
518 for those for sustaining life span. The balance between reproduction and survival is central to
519 the life history of all species and we hope that our search model, targeted at understanding
520 this trade-off in *M. jurtina*, will provide a useful route to evaluating how butterflies and other
521 species maximize their fitness given the resources they utilize and the constraints acting on
522 their mobility and perception. Our movement model demonstrated that the different methods
523 of incorporating interindividual variability have large effects on movement predictions. In
524 particular, we identified the challenge of disentangling intraspecific variation from context-
525 specific behavioural modes. Further work attempting to evaluate butterfly movement in light
526 of these concepts is likely to allow better integration of the wealth of behavioural information
527 on butterflies when investigating aspects of their movement ecology such as habitat use,
528 optimal foraging and dispersal.

529

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536

537 **References**

538 Agostinelli, C., & Lund, U. (2017). R package ‘circular’: Circular statistics (version 0.4-93).

539 R Package. Retrieved from <https://r-forge.r-project.org/projects/circular/>

540 Alcock, J. (1985). Hilltopping in the nymphalid butterfly *Chlosyne californica* (Lepidoptera).

541 *American Midland Naturalist*, 113, 69–75.

542 Alexander, R. M. (2003). *Principles of animal locomotion*. Princeton University Press.

543 Avgar, T., Kuefler, D., & Fryxell, J. M. (2011). Linking Rates of Diffusion and Consumption

544 in Relation to Resources. *The American Naturalist*, 178(2), 182–190.

545 <https://doi.org/10.1086/660825>

546 Bauduin, S., McIntire, E. J. B., & Chubaty, A. M. (2019). NetLogoR: a package to build and

547 run spatially explicit agent-based models in R. *Ecography*, 42(11), 1841–1849.

548 <https://doi.org/10.1111/ecog.04516>

549 Bergman, M., Gotthard, K., Berger, D., Olofsson, M., Kemp, D. J., & Wiklund, C. (2007).

550 Mating success of resident versus non-resident males in a territorial butterfly.

551 *Proceedings of the Royal Society B: Biological Sciences*, 274(1618), 1659–1665.

552 <https://doi.org/10.1098/rspb.2007.0311>

553 Börger, L., Dalziel, B. D., & Fryxell, J. M. (2008). Are there general mechanisms of animal

554 home range behaviour? A review and prospects for future research. *Ecology Letters*,

555 11(6), 637–650. <https://doi.org/10.1111/j.1461-0248.2008.01182.x>

556 Brakefield, P. M. (1982a). Ecological Studies on the Butterfly *Maniola jurtina* in Britain. I.
557 Adult Behaviour, Microdistribution and Dispersal. *Journal of Animal Ecology*, 51(3),
558 713. <https://doi.org/10.2307/4000>

559 Brakefield, P. M. (1982b). Ecological Studies on the Butterfly *Maniola jurtina* in Britain. II.
560 Population Dynamics: The Present Position. *Journal of Animal Ecology*, 51(3), 727.
561 <https://doi.org/10.2307/4001>

562 Breed, G. A., Jonson, I. D., Myers, R. A., Bowen, W. D., & Leonard, M. L. (2009). Sex-
563 specific, seasonal foraging tactics in adult gray seals (*Halichoerus grypus*) are revealed
564 by behaviour discriminating state-space models. *Ecology*, 90(11), 3209–3221.

565 Brown, L. M., & Crone, E. E. (2016). Individual variation changes dispersal distance and
566 area requirements of a checkerspot butterfly. *Ecology*, 97(1), 106–115.
567 <https://doi.org/10.1002/ecy.1216>

568 Brown, W. D., & Alcock, J. (1990). Hilltopping by the red admiral butterfly: Mate searching
569 alongside congeners. *Journal of Research on the Lepidoptera*, 29(1), 1–10.

570 Cant, E., Smith, A., Reynolds, D., & Osborne, J. (2005). Tracking butterfly flight paths
571 across the landscape with harmonic radar. *Proceedings of the Royal Society B:*
572 *Biological Sciences*, 272(1565), 785–790. <https://doi.org/10.1098/rspb.2004.3002>

573 Charnov, E. L. (1976). Optimal foraging, the marginal value theorem. *Theoretical Population*
574 *Biology*, 9(2), 129–136. [https://doi.org/10.1016/0040-5809\(76\)90040-X](https://doi.org/10.1016/0040-5809(76)90040-X)

575 Chittka, L., Dyer, A. G., Bock, F., & Dornhaus, A. (2003). Bees trade off foraging speed for
576 accuracy. *Nature*, 424(6947), 388–388. <https://doi.org/10.1038/424388a>

577 Chittka, L., Skorupski, P., & Raine, N. E. (2009). Speed–accuracy tradeoffs in animal
578 decision making. *Trends in Ecology & Evolution*, 24(7), 400–407.

579 Conradt, L., Bodsworth, E. J., Roper, T. J., & Thomas, C. D. (2000). Non-random dispersal
580 in the butterfly *Maniola jurtina* : implications for metapopulation models. *Proceedings*
581 *of the Royal Society of London. Series B: Biological Sciences*, 267(1452), 1505–1510.
582 <https://doi.org/10.1098/rspb.2000.1171>

583 Conradt, L., & Roper, T. J. (2006). Nonrandom movement behavior at habitat boundaries in
584 two butterfly species: Implications for dispersal. *Ecology*, 87(1), 125–132.
585 <https://doi.org/10.1890/05-0413>

586 Delattre, T., Burel, F., Humeau, A., Stevens, V. M., Vernon, P., & Baguette, M. (2010).
587 Dispersal mood revealed by shifts from routine to direct flights in the meadow brown
588 butterfly *Maniola jurtina*. *Oikos*, 119(12), 1900–1908. [https://doi.org/10.1111/j.1600-](https://doi.org/10.1111/j.1600-0706.2010.18615.x)
589 [0706.2010.18615.x](https://doi.org/10.1111/j.1600-0706.2010.18615.x)

590 Dennis, R. L. H. (1982). Mate location strategies in the wall brown butterfly, *Lasiommata*
591 *megea* (L.) (Lepidoptera: Satyridae): wait or seek? *Entomologist's Record and Journal*
592 *of Variation*, 94, 209-214.

593 Dennis, R. L. H. (1992). *Ecology of butterflies in Britain*. Oxford University Press.

594 Dennis, R. L. H., & Hardy, P. B. (2007). Support for mending the matrix: resource seeking
595 by butterflies in apparent non-resource zones. *Journal of Insect Conservation*, 11(2),
596 157–168. <https://doi.org/10.1007/s10841-006-9032-y>

597 Dennis, R. L. H., & Shreeve, T. G. (1988). Hostplant-habitat structure and the evolution of
598 butterfly mate-locating behaviour. *Zoological Journal of the Linnean Society*, 94(4),
599 301–318.

600 Dias, M. P., Granadeiro, J. P., & Palmeirim, J. M. (2009). Searching behaviour of foraging
601 waders: does feeding success influence their walking? *Animal Behaviour*, 77(5), 1203–

602 1209.

603 Dover, J. W. (1989). A method for recording and transcribing observations of butterfly
604 behaviour. *Entomologist's Gazette*, 40, 95–100.

605 Dowdeswell, W. (1981). *The life of the meadow brown*. Butler & Tanner.

606 Evans, L. C., Sibly, R. M., Thorbek, P., Sims, I., Oliver, T. H., & Walters, R. J. (2019a).
607 Integrating the influence of weather into mechanistic models of butterfly movement.
608 *Movement Ecology*, 7(1), 24. <https://doi.org/10.1186/s40462-019-0171-7>

609 Evans, L. C., Sibly, R. M., Thorbek, P., Sims, I., Oliver, T. H., & Walters, R. J. (2019b).
610 Quantifying the effectiveness of agri-environment schemes for a grassland butterfly
611 using individual-based models. *Ecological Modelling*, 411, 108798.
612 <https://doi.org/10.1016/j.ecolmodel.2019.108798>

613 Evans, L. C., Sibly, R. M., Thorbek, P., Sims, I., Oliver, T. H., & Walters, R. J. (2020a).
614 Behavior underpins the predictive power of a trait-based model of butterfly movement.
615 *Ecology and Evolution*, 10(7), 3200–3208. <https://doi.org/10.1002/ece3.5957>

616 Evans, L. C., Sibly, R. M., Thorbek, P., Sims, I., Oliver, T. H., & Walters, R. J. (2020b). The
617 importance of including habitat-specific behaviour in models of butterfly movement.
618 *Oecologia*, (0123456789). <https://doi.org/10.1007/s00442-020-04638-4>

619 Evans, L. C., Sims, I., Sibly, R. M., Thorbek, P., Oliver, T. H., & Walters, R. J. (2019). Data
620 on the movement behaviour of four species of grassland butterfly. *Data in Brief*, 27,
621 104611. <https://doi.org/10.1016/j.dib.2019.104611>

622 Forester, J. D., Ives, A. R., Turner, M. G., Anderson, D. P., Fortin, D., Beyer, H. L., ...
623 Boyce, M. S. (2007). State–space models link elk movement patterns to landscape
624 characteristics in Yellowstone national park. *Ecological Monographs*, 77(2), 285–299.

625 <https://doi.org/10.1890/06-0534>

626 Fownes, S., & Roland, J. (2002). Effects of meadow suitability on female behaviour in the
627 alpine butterfly *Parnassius smintheus*. *Ecological Entomology*, 27(4), 457–466.
628 <https://doi.org/10.1046/j.1365-2311.2002.00426.x>

629 Fox, R., Brereton, T. M., Asher, J., August, T. A., Botham, M. S., Bourn, N. A. D., ...
630 Harrower, C. A. (2015). *The state of the UK's butterflies 2015*. Butterfly
631 Conservation/Centre for Ecology and Hydrology.

632 Franke, A., Caelli, T., & Hudson, R. J. (2004). Analysis of movements and behavior of
633 caribou (*Rangifer tarandus*) using hidden Markov models. *Ecological Modelling*,
634 173(2–3), 259–270. <https://doi.org/10.1016/j.ecolmodel.2003.06.004>

635 Fryxell, J. M., Hazell, M., Borger, L., Dalziel, B. D., Haydon, D. T., Morales, J. M., ...
636 Rosatte, R. C. (2008). Multiple movement modes by large herbivores at multiple
637 spatiotemporal scales. *Proceedings of the National Academy of Sciences*, 105(49),
638 19114–19119. <https://doi.org/10.1073/pnas.0801737105>

639 Gurarie, E., Anderson, J. J., & Zabel, R. W. (2009). Continuous models of population-level
640 heterogeneity inform analysis of animal dispersal and migration. *Ecology*, 90(8), 2233–
641 2242. <https://doi.org/10.1890/08-0359.1>

642 Gurarie, E., Andrews, R. D., & Laidre, K. L. (2009). A novel method for identifying
643 behavioural changes in animal movement data. *Ecology Letters*, 12(5), 395–408.
644 <https://doi.org/10.1111/j.1461-0248.2009.01293.x>

645 Hartigan, J. A., & Wong, M. A. (1979). Algorithm AS 136: A K-Means Clustering
646 Algorithm. *Applied Statistics*, 28(1), 100. <https://doi.org/10.2307/2346830>

647 Haskell, D. G. (1997). Experiments and a model examining learning in the area-restricted

648 search behavior of ferrets (*Mustela putorius furo*). *Behavioral Ecology*, 8(4), 448–449.
649 <https://doi.org/10.1093/beheco/8.4.448>

650 Hebblewhite, M., & Haydon, D. T. (2010). Distinguishing technology from biology: a critical
651 review of the use of GPS telemetry data in ecology. *Philosophical Transactions of the*
652 *Royal Society B: Biological Sciences*, 365(1550), 2303–2312.

653 Holyoak, M., Casagrandi, R., Nathan, R., Revilla, E., & Spiegel, O. (2008). Trends and
654 missing parts in the study of movement ecology. *Proceedings of the National Academy*
655 *of Sciences*, 105(49), 19060–19065. <https://doi.org/10.1073/pnas.0800483105>

656 Jonsen, I. D., Myers, R. A., & James, M. C. (2006). Robust hierarchical state-space models
657 reveal diel variation in travel rates of migrating leatherback turtles. *Journal of Animal*
658 *Ecology*, 75(5), 1046–1057. <https://doi.org/10.1111/j.1365-2656.2006.01129.x>

659 Kallioniemi, E., Zannese, A., Tinker, J. E., & Franco, A. M. A. (2014). Inter- and intra-
660 specific differences in butterfly behaviour at boundaries. *Insect Conservation and*
661 *Diversity*, 7(3), 232–240. <https://doi.org/10.1111/icad.12046>

662 Kassambara, A., & Mundt, F. (2017). Factoextra: extract and visualize the results of
663 multivariate data analyses. R Package Version 1.0.5. Retrieved from [https://cran.r-](https://cran.r-project.org/web/packages/factoextra/factoextra.pdf)
664 [project.org/web/packages/factoextra/factoextra.pdf](https://cran.r-project.org/web/packages/factoextra/factoextra.pdf)

665 Korösi, Á., Örvössy, N., Batáry, P., Kövér, S., & Peregovits, L. (2008). Restricted within-
666 habitat movement and time-constrained egg laying of female *Maculinea rebeli*
667 butterflies. *Oecologia*, 156(2), 455–464. <https://doi.org/10.1007/s00442-008-0986-1>

668 Lebeau, J., Wesselingh, R. A., & Van Dyck, H. (2015). Butterfly Density and Behaviour in
669 Uncut Hay Meadow Strips: Behavioural Ecological Consequences of an Agri-
670 Environmental Scheme. *PLoS One*, 10(8), e0134945.

671 <https://doi.org/10.1371/journal.pone.0134945>

672 Lebeau, J., Wesselingh, R. A., & Van Dyck, H. (2016a). Floral resource limitation severely
673 reduces butterfly survival, condition and flight activity in simplified agricultural
674 landscapes. *Oecologia*, *180*(2), 421–427. <https://doi.org/10.1007/s00442-015-3492-2>

675 Lebeau, J., Wesselingh, R. A., & Van Dyck, H. (2016b). Nectar resource limitation affects
676 butterfly flight performance and metabolism differently in intensive and extensive
677 agricultural landscapes. *Proceedings of the Royal Society B: Biological Sciences*,
678 *283*(1830), 20160455. <https://doi.org/10.1098/rspb.2016.0455>

679 Lebeau, J., Wesselingh, R. A., & Van Dyck, H. (2017). Flower use of the butterfly *Maniola*
680 *jurtina* in nectar-rich and nectar-poor grasslands: a nectar generalist with a strong
681 preference? *Insect Conservation and Diversity*, *10*(3), 258–270.
682 <https://doi.org/10.1111/icad.12222>

683 Louzao, M., Wiegand, T., Bartumeus, F., & Weimerskirch, H. (2014). Coupling
684 instantaneous energy-budget models and behavioural mode analysis to estimate optimal
685 foraging strategy: an example with wandering albatrosses. *Movement Ecology*, *2*(1), 8.
686 <https://doi.org/10.1186/2051-3933-2-8>

687 Maechler, M., Rousseeuw, P., Struyf, A., Hubert, M., & Hornik, K. (2019). cluster: Cluster
688 Analysis Basics and Extensions. R Package Version 2.1.0. Retrieved from [https://cran.r-](https://cran.r-project.org/web/packages/cluster/cluster.pdf)
689 [project.org/web/packages/cluster/cluster.pdf](https://cran.r-project.org/web/packages/cluster/cluster.pdf)

690 Mair, L., Thomas, C. D., Franco, A. M. A., & Hill, J. K. (2015). Quantifying the activity
691 levels and behavioural responses of butterfly species to habitat boundaries. *Ecological*
692 *Entomology*, *40*(6), 823–828. <https://doi.org/10.1111/een.12248>

693 Mattila, A. L. K. (2015). Thermal biology of flight in a butterfly: genotype, flight

694 metabolism, and environmental conditions. *Ecology and Evolution*, 5(23), 5539–5551.
695 <https://doi.org/10.1002/ece3.1758>

696 McClintock, B. T., London, J. M., Cameron, M. F., & Boveng, P. L. (2017). Bridging the
697 gaps in animal movement: hidden behaviors and ecological relationships revealed by
698 integrated data streams. *Ecosphere*, 8(3), e01751. <https://doi.org/10.1002/ecs2.1751>

699 Morales, J. M., & Ellner, S. P. (2002). Scaling up animal movements in heterogeneous
700 landscapes: the importance of behavior. *Ecology*, 83(8), 2240–2247.

701 Morales, J. M., Haydon, D. T., Frair, J., Holsinger, K. E., & Fryxell, J. M. (2004). Extracting
702 more out of relocation data: building movement models as mixtures of random walks.
703 *Ecology*, 85(9), 2436–2445. <https://doi.org/10.1890/03-0269>

704 Nathan, R., Getz, W. M., Revilla, E., Holyoak, M., Kadmon, R., Saltz, D., & Smouse, P. E.
705 (2008). A movement ecology paradigm for unifying organismal movement research.
706 *Proceedings of the National Academy of Sciences*, 105(49), 19052–19059.
707 <https://doi.org/10.1073/pnas.0800375105>

708 Niitepold, K. (2010). Genotype by temperature interactions in the metabolic rate of the
709 Glanville fritillary butterfly. *Journal of Experimental Biology*, 213(7), 1042–1048.
710 <https://doi.org/10.1242/jeb.034132>

711 Niitepõld, K., & Boggs, C. L. (2015). Effects of Increased Flight on the Energetics and Life
712 History of the Butterfly *Speyeria mormonia*. *PLoS One*, 10(10), e0140104.
713 <https://doi.org/10.1371/journal.pone.0140104>

714 Niven, J. E., & Scharlemann, J. P. W. (2005). Do insect metabolic rates at rest and during
715 flight scale with body mass? *Biology Letters*, 1(3), 346–349.
716 <https://doi.org/10.1098/rsbl.2005.0311>

717 Odendaal, F. J., Turchin, P., Stermitz, F. R., Odendaal, F. J., Turchin, P., & Stermitz, F. R.
718 (1989). Influence of Host-Plant Density and Male Harassment on the Distribution of
719 Female *Euphydryas anicia* (Nymphalidae). *Oecologia*, 78(2), 283–288.

720 Ouin, A., Martin, M., & Burel, F. (2008). Agricultural landscape connectivity for the meadow
721 brown butterfly (*Maniola jurtina*). *Agriculture, Ecosystems & Environment*, 124(3–4),
722 193–199. <https://doi.org/10.1016/j.agee.2007.09.010>

723 Ovaskainen, O., Luoto, M., Ikonen, I., Rekola, H., Meyke, E., & Kuussaari, M. (2008). An
724 Empirical Test of a Diffusion Model: Predicting Clouded Apollo Movements in a Novel
725 Environment. *The American Naturalist*, 171(5), 610–619.
726 <https://doi.org/10.1086/587070>

727 Ovaskainen, O., Rekola, H., Meyke, E., & Arjas, E. (2008). Bayesian methods for analyzing
728 movements in heterogeneous landscapes from mark-recapture data. *Ecology*, 89(2),
729 542–554. <https://doi.org/10.1890/07-0443.1>

730 Ovaskainen, O., Smith, A. D., Osborne, J. L., Reynolds, D. R., Carreck, N. L., Martin, A. P.,
731 ... Hanski, I. (2008). Tracking butterfly movements with harmonic radar reveals an
732 effect of population age on movement distance. *Proceedings of the National Academy of*
733 *Sciences of the United States of America*, 105(49), 19090–19095.
734 <https://doi.org/10.1073/pnas.0802066105>

735 Patterson, T. A., Parton, A., Langrock, R., Blackwell, P. G., Thomas, L., & King, R. (2017).
736 Statistical modelling of individual animal movement: an overview of key methods and a
737 discussion of practical challenges. *AStA Advances in Statistical Analysis*, 101(4), 399–
738 438. <https://doi.org/10.1007/s10182-017-0302-7>

739 Patterson, T. A., Thomas, L., Wilcox, C., Ovaskainen, O., & Matthiopoulos, J. (2008). State-
740 space models of individual animal movement. *Trends in Ecology & Evolution*, 23(2), 87-94.

741 <https://doi.org/10.1016/j.tree.2007.10.009>

742 Polic, D., Fiedler, K., Nell, C., & Grill, A. (2014). Mobility of ringlet butterflies in high-
743 elevation alpine grassland: effects of habitat barriers, resources and age. *Journal of*
744 *Insect Conservation*, 18(6), 1153–1161. <https://doi.org/10.1007/s10841-014-9726-5>

745 R Core Team (2019). *R: A language and environment for statistical computing*. R Foundation
746 for Statistical Computing.

747 Ripley, B., Venables, W., & Ripley, M. B. (2016). Package ‘nnet.’ R Package Version 7.
748 Retrieved from <https://cran.r-project.org/web/packages/nnet/nnet.pdf>

749 Roland, J., Keyghobadi, N., & Fownes, S. (2000). Alpine *Parnassius* butterfly dispersal:
750 Effects of landscape and population size. *Ecology*, 81(6), 1642–1653.
751 [https://doi.org/10.1890/0012-9658\(2000\)081\[1642:APBDEO\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2000)081[1642:APBDEO]2.0.CO;2)

752 Root, R. B., & Kareiva, P. M. (1984). The search for resources by cabbage butterflies (*Pieris*
753 *rapae*): ecological consequences and adaptive significance of Markovian movements in
754 a patchy environment. *Ecology*. <https://doi.org/10.2307/1939467>

755 Rousseeuw, P. J. (1987). Silhouettes: A graphical aid to the interpretation and validation of
756 cluster analysis. *Journal of Computational and Applied Mathematics*, 20(C), 53–65.
757 [https://doi.org/10.1016/0377-0427\(87\)90125-7](https://doi.org/10.1016/0377-0427(87)90125-7)

758 Scali, V. (1971). Imaginal Diapause and Gonadal Maturation of *Maniola jurtina*
759 (Lepidoptera: Satyridae) from Tuscany. *Journal of Animal Ecology*, 40(2), 467.
760 <https://doi.org/10.2307/3255>

761 Schick, R. S., Loarie, S. R., Colchero, F., Best, B. D., Boustany, A., Conde, D. A., ... Clark,
762 J. S. (2008). Understanding movement data and movement processes: Current and
763 emerging directions. *Ecology Letters*, 11(12), 1338–1350.

764 <https://doi.org/10.1111/j.1461-0248.2008.01249.x>

765 Schneider, C. (2003). The influence of spatial scale on quantifying insect dispersal: an
766 analysis of butterfly data. *Ecological Entomology*, 28(2), 252–256.
767 <https://doi.org/10.1046/j.1365-2311.2003.00495.x>

768 Schneider, C., Dover, J., & Fry, G. L. A. (2003). Movement of two grassland butterflies in
769 the same habitat network: the role of adult resources and size of the study area.
770 *Ecological Entomology*, 28(2), 219–227. [https://doi.org/10.1046/j.1365-](https://doi.org/10.1046/j.1365-2311.2003.00494.x)
771 [2311.2003.00494.x](https://doi.org/10.1046/j.1365-2311.2003.00494.x)

772

773 Schtickzelle, N., Joiris, A., Dyck, H. Van, & Baguette, M. (2007). Quantitative analysis of
774 changes in movement behaviour within and outside habitat in a specialist butterfly. *BMC*
775 *Evolutionary Biology*, 7(1), 1–15. <https://doi.org/10.1186/1471-2148-7-4>

776 Schultz, C. B. (1998). Dispersal Behavior and Its Implications for Reserve Design in a Rare
777 Oregon Butterfly. *Conservation Biology*, 12(2), 284–292. [https://doi.org/10.1046/j.1523-](https://doi.org/10.1046/j.1523-1739.1998.96266.x)
778 [1739.1998.96266.x](https://doi.org/10.1046/j.1523-1739.1998.96266.x)

779 Schultz, C. B., & Crone, E. E. (2001). Edge-Mediated Dispersal Behavior in a Prairie
780 Butterfly. *Ecology*, 82(7), 1879. <https://doi.org/10.2307/2680054>

781 Schultz, C. B., Franco, A. M. a, & Crone, E. E. (2012). Response of butterflies to structural
782 and resource boundaries. *Journal of Animal Ecology*, 81(3), 724–734.
783 <https://doi.org/10.1111/j.1365-2656.2011.01947.x>

784 Scott, J. A. (1974). Mate-Locating Behavior of Butterflies. *American Midland Naturalist*,
785 91(1), 103. <https://doi.org/10.2307/2424514>

786 Seidel, D. P., Dougherty, E., Carlson, C., & Getz, W. M. (2018). Ecological metrics and

787 methods for GPS movement data. *International Journal of Geographical Information*
788 *Science*, 32(11), 2272–2293.

789 Shreeve, T. G. (1984). Habitat selection, mate location, and microclimatic constraints on the
790 activity of the speckled wood butterfly *Pararge aegeria*. *Oikos*, 42(3), 371–377.
791 <https://doi.org/10.2307/3544407>

792 Shreeve, T. G. (1992). Adult behaviour. In R. L. H. Dennis (Ed.), *The ecology of butterflies*
793 *of Britain* (pp. 22–45). Oxford University Press.

794 Sih, A., Bell, A., & Johnson, J. C. (2004). Behavioral syndromes: An ecological and
795 evolutionary overview. *Trends in Ecology & Evolution*, 19(7), 372–378.
796 <https://doi.org/10.1016/j.tree.2004.04.009>

797 Singh, N. J., Börger, L., Dettki, H., Bunnefeld, N., & Ericsson, G. (2012). From migration to
798 nomadism: movement variability in a northern ungulate across its latitudinal range.
799 *Ecological Applications*, 22(7), 2007–2020. <https://doi.org/10.1890/12-0245.1>

800 Skalski, G. T., & Gilliam, J. F. (2003). A Diffusion-Based Theory of Organism Dispersal in
801 Heterogeneous Populations. *The American Naturalist*, 161(3), 441–458.
802 <https://doi.org/10.1086/367592>

803 Smith, J. N. M. (1974). The Food Searching Behaviour of Two European Thrushes.
804 *Behaviour*, 48(1–4), 276–301. <https://doi.org/10.1163/156853974X00363>

805 Spiegel, O., Leu, S. T., Bull, C. M., & Sih, A. (2017). What’s your move? Movement as a
806 link between personality and spatial dynamics in animal populations. *Ecology Letters*,
807 20(1), 3–18. <https://doi.org/10.1111/ele.12708>

808 Stevens, V. M., Trochet, A., Van Dyck, H., Clobert, J., & Baguette, M. (2012). How is
809 dispersal integrated in life histories: a quantitative analysis using butterflies. *Ecology*

810 *Letters*, 15(1), 74–86. <https://doi.org/10.1111/j.1461-0248.2011.01709.x>

811 Stevens, V. M., Turlure, C., & Baguette, M. (2010). A meta-analysis of dispersal in
812 butterflies. *Biological Reviews*, 85(3), 625–642. <https://doi.org/10.1111/j.1469->
813 185X.2009.00119.x

814 Takeuchi, T. (2010). Mate-locating behavior of the butterfly *Lethe diana* (Lepidoptera:
815 Satyridae): do males diurnally or seasonally change their mating strategy? *Zoological*
816 *Science*, 27(10), 821–825.

817 Thomas, J. (2010). *Butterflies of Britain and Ireland*. British Wildlife Publishing.

818 Tinbergen, N. (1963). On aims and methods of ethology. *Zeitschrift für Tierpsychologie*,
819 20(4), 410–433.

820 Tukey, J. W. (1949). Comparing individual means in the analysis of variance. *Biometrics*,
821 5(2), 99–114.

822 Turchin, P. (1991). Translating Foraging Movements in Heterogeneous Environments into
823 the Spatial Distribution of Foragers. *Ecology*, 72(4), 1253–1266.

824 Van Swaay, C. A. M., Dennis, E. B., Schmucki, R., Sevilleja, C. G., Balalaikins, M., Botham,
825 M., ... Carlisle, B. (2019). The EU Butterfly Indicator for Grassland species: 1990-
826 2017: Technical Report. *Butterfly Conservation Europe & ABLE/EBMS*.

827 Vande Velde, L., & Van Dyck, H. (2013). Lipid economy, flight activity and reproductive
828 behaviour in the speckled wood butterfly: on the energetic cost of territory holding.
829 *Oikos*, 122(4), 555–562. <https://doi.org/10.1111/j.1600-0706.2012.20747.x>

830 Walters, R. J., Hassall, M., Telfer, M. G., Hewitt, G. M., & Palutikof, J. P. (2006). Modelling
831 dispersal of a temperate insect in a changing climate. *Proceedings of the Royal Society*
832 *B: Biological Sciences*, 273(1597), 2017–2023. <https://doi.org/10.1098/rspb.2006.3542>

- 833 Weimerskirch, H., Bonadonna, F., Bailleul, F., Mabile, G., Dell’Omo, G., & Lipp, H.-P.
834 (2002). GPS tracking of foraging albatrosses. *Science*, 295(5558), 1259.
- 835 Wickman, P.-C. (1985). The influence of temperature on the territorial and mate locating
836 behaviour of the small heath butterfly, *Coenonympha pamphilus* (L.) (Lepidoptera:
837 Satyridae). *Behavioral Ecology and Sociobiology*, 16(3), 233–238.
838 <https://doi.org/10.1007/BF00310985>
- 839 Wiklund, C. (2003). Sexual selection and the evolution of butterfly mating systems. In C. L.
840 Boggs, W. B. Watt, & P. R. Ehrlich (Eds.), *Butterflies, ecology and evolution taking*
841 *flight* (pp. 67–90). University of Chicago Press.
- 842 Williams, H. J., Taylor, L. A., Benhamou, S., Bijleveld, A. I., Clay, T. A., Grissac, S., ...
843 Börger, L. (2020). Optimizing the use of biologgers for movement ecology research.
844 *Journal of Animal Ecology*, 89(1), 186–206. <https://doi.org/10.1111/1365-2656.13094>
- 845 Woods Jr., W. A., Wood, C. A. L., Ebersole, J., & Stevenson, R. D. (2010). Metabolic Rate
846 Variation over Adult Lifetime in the Butterfly *Vanessa cardui* (Nymphalidae:
847 Nymphalinae): Aging, Feeding, and Repeatability. *Physiological and Biochemical*
848 *Zoology*, 83(5), 858–868. <https://doi.org/10.1086/656216>
- 849 Zalucki, M. P., & Kitching, R. L. (1982). The Analysis and Description of Movement in
850 Adult *Danaus plexippus* L. (Lepidoptera: Danainae). *Behaviour*, 80(3–4), 174–197.
851 <https://doi.org/10.1163/156853982X00346>
- 852 Zollner, P. A., & Lima, S. L. (2005). Behavioral tradeoffs when dispersing across a patchy
853 landscape. *Oikos*, 108(2), 219–230.

854 **Table 1.** Coefficients (\pm SEs) from the multinomial regression

	Intercept	Sex (male)	Habitat (nectar- rich)	Air temperature
3 (High-inactive)	-	-	-	-
1 (High-bask)	-4.85 (1.29)***	-0.33 (0.36)	1.93 (0.76)*	0.08 (0.05)
2 (High-flight)	-0.42 (1.03)	3.48 (0.49)***	-2.24 (0.38)***	-0.07 (0.05)
4 (High-nectar)	-7.86 (23.79)	-0.79 (0.33)*	9.91 (23.77)	-0.12 (0.05)*

855 Coefficients show changes in log odd ratios of a time budget occurring in a cluster relative to
 856 the baseline cluster for a unit change in the predictors. The baseline here is the inactive group
 857 ('High-inactive'). Significance scores for coefficient estimates were produced using a two-
 858 tailed Wald test.

859 * $P < 0.05$; *** $P < 0.001$.

860

861

862 **Table 2.** Coefficients from the multinomial regression of clustering within nectar-rich
 863 habitats

	Female		Male	
	Intercept	Insolation	Intercept	Insolation
High-inactive	-	-	-	-
High-bask	-1.01***	2.17 x 10 ⁻⁶	-1.67***	2.43 x 10 ⁻⁵
High-nectar	-1.5***	9.46 x 10 ⁻⁶ ***	-3.67***	2.28 x 10 ⁻⁵ ***
High-flight †	--	--	-3.8***	2.56 x 10 ⁻⁵ ***
Mixed †	--	--	-1.93***	1.02 x 10 ⁻⁵ ***

864 Coefficients show changes in log odd ratios of a time budget occurring in a cluster relative to
 865 the baseline cluster for a unit change in the predictors. The baseline here is the inactive group
 866 ('High-inactive'). Significance scores for coefficient estimates were produced using a two-
 867 tailed Wald test.

868 *** $P < 0.001$.

869 † Cluster only observed in males.

870

871

872

873 **Figure 1.** The average duration of behaviours within clusters and the proportion of
874 individuals grouped in clusters across sex and habitat types. Left-hand panels (a-d) show
875 cluster groups with bars representing the mean proportions of time the behaviour was
876 performed in the cluster, middle panels show the proportion of the different sexes grouped in
877 the cluster, and the right-hand panels show the proportion of the habitat types (nectar-poor
878 and nectar-rich) in which the cluster was observed. ‘Ovi’ refers to oviposition an activity rare
879 across all clusters.

880

881 **Figure 2.** Movement parameters in selected cluster groups. (a) Step distances and (b) turning
882 angles for males in the ‘high-nectar’ versus ‘high-flight’ clusters. (c) Step distances and (d)
883 turning angles for females in the ‘high-nectar’ versus ‘high-inactive’ clusters. Pairings were
884 chosen as examples where both step distances and turning angles were significantly different
885 between the groups.

886

887 **Figure 3.** Comparison of displacement predictions from the random-walk models. (a) Males
888 and (b) females.

889

890 **Figure 4.** (a) The optimal amount of time butterflies should spend in exclusive search T_{sp} ,
891 given the rate of resource diminishment c and the relative search effectiveness of exclusive
892 search over normal behaviour B . (b) The optimal time when $c = 0$ and (c) the optimal time
893 when $c = 1$ representing no resource diminishment and total resource diminishment at
894 maximal life span, respectively.