klimaat voor ruimte
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THE INFLUENCE OF TEMPERATURE AND SOLAR RADIATION ON THE BEHAVIOUR OF BUTTERFLIES

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Fig 1. Study species (from left to right): *Melitaea athalia, Coenonympha pamphilus, Plebejus argus* and *Maniola jurtina.*

Introduction

The Netherlands will soon face temperature rise both in summer and winter as well as higher frequency of dry periods and extreme rainfall events (Bresser et al., 2005). These changes have an immediate effect on the butterfly behaviour as they are ectothermic animals. Studies of behaviour and especially dispersal are of great importance for population viability, especially in fragmented landscape where migration pressures are large.

Research question: How do the temperature and other weather parameters influence the behaviour of the four butterfly species?

Research hypothesis: There is a thermal optimum within which butterflies are most active (flying a lot); in temperatures lower than optimal they spend more time resting and basking and in temperatures higher than optimal they display heat-avoiding behaviour. Wind is expected to have an adverse effect on the activity.

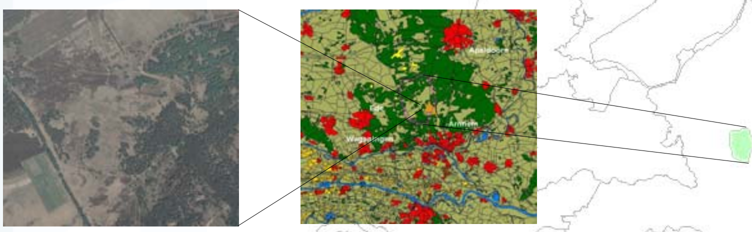

Fig.2 Study area comprises heathlands and meadows located in the National Park De Hoge Veluwe

Data collection

A time-budget study of 4 species (fig 1) was conducted in the National Park 'De Hoge Veluwe' (fig 2) in summer 2006. With every observation the environmental factors like air temperature, radiation, wind speed and cloud cover were measured. Butterflies were caught, sexed, wing-marked (fig 3), released and followed (keeping a distance of 2-5 m) by the observer with GPS. Data on behaviour (feeding, flying, resting or basking), time and position were collected.

The nature of the data ('time-to-event' data with censors) implied that the statistical tool used was **survival analysis**. The study unit was **a bout**, which is the time of uninterrupted behaviour (Haccou et Meelis, 1992). Some bouts were censored - the end or the beginning of the observation has not been recorded. In this study **right-censoring** occurred when the observation ended or when the butterfly was lost from sight before 30 minutes had passed.

Results

The model analyses bout lengths and therewith the tendency to stop a bout. In almost all cases the duration of the flying bouts increased as the temperature and solar radiation increased, which is in line with our research hypothesis (fig 4). Taking into account the significant results, there was always positive correlation between active bouts duration and temperature or solar radiation increase, whereas passive bouts were usually negatively correlated with these variables. In only three cases we were able to prove the presence of an optimum. Sex proved to have no influence on the results. Results for *C. pamphilus* are presented.

Fig 3. Wing-marked *C. pamphilus* released from the net.

	Covariates:	temp(1)	temp(2)	temp(3)	sol	wind
Flying bouts (251)	**β**	-0.794	-0.796	-0.002	n.incl	n.incl
	HR	0.452	0.451	0.998		
	Wald	9.530**	9.213**	0.000		
Active bouts (242)	**β**	-0.561	-0.460	0.101	n.incl	0.187
	HR	0.571	0.631	1.106		1.205
	Wald	4.245*	2.990	0.440		1.571
Passive bouts (265)	**β**	0.685	0.351	-0.334	0.642	n.incl
	HR	1.983	1.420	0.716	1.901	
	Wald	5.542*	1.259	5.579*	10.817**	

Table 1 Results of the Cox's regression analysis for *C. pamphilus*. β - estimated regression coefficient, HR – hazard ratio, Wald – Wald statistic (*P<=0.05 **P<=0.01 ***P<<0.001), temp(1) – air temperature, contrast between 16-19°C and 20-24°C, temp(2) – air temperature, contrast between 16-19°C and 25-31°C, temp(3) – air temperature, contrast between 20-24°C and 25-31°C, sol – solar radiation expressed in temperature difference of black and white surface, wind – wind speed, n.incl – not included in the Cox model because of insignificant log-rank test. Numbers in the brackets indicate the number of observations

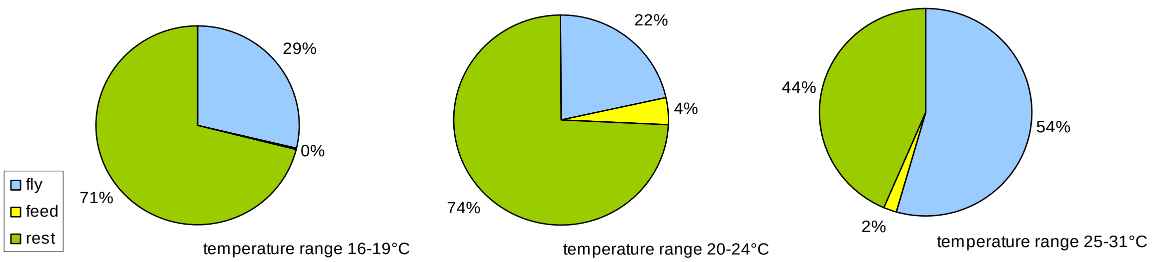

Fig 5. Total time allocated by *C. pamphilus* to flying is the highest in the highest temperature range

Survival analysis of the data

Data sets which met the proportionality assumption (were significantly different according to log-rank test) were used in Cox regression. The proportional hazards model was used to analyse which weather factors are increasing or decreasing the tendency of a butterfly to terminate a bout. It is assumed that the butterflies have a basic tendency to stop a behaviour (baseline hazard), which is reset after each transition. The observed hazard rate is therefore the product of the baseline hazard and a factor that gives the joint effect of all covariates (temperature, solar radiation, and wind as categorical covariates) Next to survival analysis, the total time allocations to each of the behaviours were calculated (fig 5).

General form of the model:

$$h(t;x) = h_0(t) \cdot \exp\left(\sum_{i=1}^{p} \beta_i x_i\right)$$

where:

h(t;x) represents the observed hazard rate,

h0(t) the base-line hazard (basic tendency to stop when there is no effect of weather factors),

t the time since the last transition and

β1, …, βp the relative contributions of covariates to the observed hazard rate.

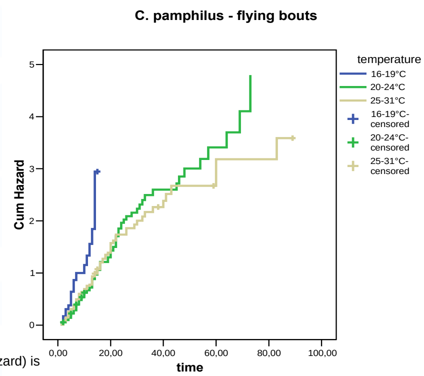

Fig 4. The tendency to stop flying (cumulative hazard) is the highest in the lowest temperature range.

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