

Review articles & Short notes

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Review of butterfly territorial behaviour and contests over mating territories**Sunil Kumaraswamy* and B. N. Balaji***University of Agricultural Sciences, Bengaluru 560065, India.***Corresponding author: sunilkumaraswamy.m@gmail.com***Introduction**

Competition for limited resources among animals, such as food, shelter, and mates, often leads to confrontations, particularly among males competing for mating territory, posing risks of injury or death. Resource holding potential (RHP), often related to body size or weaponry, influences the outcome. While game theory aids in understanding these contests, not all animals have physical adaptations for combat (Maynard Smith and Price, 1973). Despite lacking traditional weapons, butterflies compete for mating opportunities, with some establishing territories for aerial interactions and others employing patrolling strategies near food plants (Kemp and Wiklund 2001; Rutowski 1991). The cognitive limitations of butterflies raise questions about their ability to recognize rivals. This ongoing debate intrigues behavioural ecologists, offering insights into the evolution of non-aggressive contest systems (Suzuki, 1976). Butterflies utilize various strategies for mating, like vibrant colours, pheromone emissions, and territorial conflicts. Their vibrant hues aid in species recognition and mate identification, while

pheromones facilitate communication and attraction. Male butterflies initially pursue any movement but later consider factors like colour, scent, and behaviour in potential mates. Some female pheromones can be detected by males from distances of up to 10 miles. Males compete for mating opportunities, engaging in energetic disputes with rivals. Courtship involves intricate dances, with some species requiring specific displays from males. Successful courtship demands persistence and a delicate balance of sensory cues, luck, and perseverance. Additionally, some butterflies establish territories to increase their chances of finding a mate.

Mating territory

Butterflies have two primary mating strategies: "perching" and "patrolling". Patrolling males actively search for females in flight, while perching males wait for females to pass by from stationary positions. Perching sites are often associated with resources for females, but may also be located in areas with specific topographical features. Males in perching species tend to be territorial, attempting to exclude other males from their perching sites. These territories are believed to

serve as meeting points for the sexes, where mating success is assumed to be higher. However, there is limited empirical evidence supporting this assumption, with the consensus based largely on indirect observations (Takeuchi, 2017).

Territory residency and mating success

Males of *Pararge aegeria* use a perching mate-locating strategy and are found perching in large sunspots on the forest floor. If a flying object enters the sunspot area, occupied by a *P. aegeria* male, the resident male immediately takes off. He pursues the intruder to investigate what the intruding object might be (Bergman *et al.*, 2007). If the intruder is a conspecific female, a flight pursuit follows. But suppose another male enters the sunspot area, in that case, the territory resident will take off and the two will engage in a flight contest, where the winner gets sole ownership of the sunspot and the loser leaves the area and has to search for a new suitable sunspot (Davies 1978; Wickman & Wiklund 1983). So, resident males of *P. aegeria* achieves approximately twice as many mating as non-residents when virgin females of *P. aegeria* are allowed to choose between a resident and a non-resident male in a large enclosure containing one territorial sunspot (Fig.1) (Bergman *et al.*, 2007).

Why do residents receive more mating?

The success of perching males depends on the ability to detect a passing object.

However, extrinsic factors impact visual mate detection in butterflies. In a study, butterfly models varying in size and color were presented to perched males of *Asterocampa leilia* (Fig. 2A). Model type significantly influenced male response rates, with the black model prompting the highest response (87%), the white model the lowest (26%), and the grey and tan models at 52% and 60% respectively. Background type also affected response rates, with the sky background eliciting the highest response (87%) and the vegetation (45%) and sand (50%) backgrounds yielding lower responses (Fig. 2B). So, the proximate advantage of territory ownership is that light conditions and contrast greatly increase the male's ability to detect and intercept passing receptive females (Bergman *et al.*, 2015).

Can males discriminate the sex of flying conspecifics

For successful mating, males should recognize the sex of passing butterflies. When old-world swallow tail, *Papilio machaon* males were presented with motor-driven specimens that mimic the flight of butterflies, territorial males responded to flapping specimens with four sequential phases: approach, touch, courtship flight, and copulation attempt (Fig. 3); these responses were observed to be more pronounced towards fresh specimens compared to treated ones, with a preference for female specimens during prolonged interactions (Takeuchi *et al.*, 2019).

Contests over mating territory

The contest is a direct and indirect behavioral interaction that determines the ownership of an indivisible resource unit (Hardy and Briffa, 2013). Butterflies lack physical weapons and thus engage in non-contact aerial interactions for territory disputes, characterized by circling flights and followed by horizontal pursuits. Various butterfly species partake in similar aerial contests over mating territories, where a territorial male claims a specific area frequented by females. When a female enters, the male visually detects her and may give chase, sometimes leading to copulation either in flight or when both are alight. In the presence of intruding males, territorial disputes involve aerial displays and chases, often ending without physical harm, serving as contests to determine territorial ownership (Kemp and Wiklund 2001; Kemp 2013; Takeuchi 2011). This behavior is known as the 'war of attrition,' where prolonged displays establish the victor, with the earlier retreator being deemed the loser.

How these butterflies settle their disputes

As butterfly males compete for mating territory, it is necessary to know how these males settle their contests. Contests in nature are asymmetric and male–male agonistic interactions should be settled in favour of the individual with the greater fighting ability, termed resource holding potential (RHP). Winner and loser males should consistently

differ in some morphological or physiological traits (Takeuchi, 2017). Butterfly contests pose a challenge due to the uncertain costs they impose on opponents, with the actual costs remaining undetermined (Kemp and Wiklund, 2001). The territorial contest in butterflies was initially considered an example of the bourgeois strategy, which was later refuted by studies showing that territory owners could indeed regain their territory after temporarily leaving it (Davies 1978; Wickman and Wiklund 1983; Kemp and Wiklund 2004). Residency effects have been observed in butterfly territorial systems, exemplified by the extended chasing behaviour of longer-term territory holders (Takeuchi 2006a, b, 2016; Takeuchi and Honda 2009). These results were attributed to the males' minimizing risks through prolonged interaction (Takeuchi *et al.*, 2016).

Although fighting costs remain unclear, differences in morphological or physiological characteristics between territory owners and intruders have been noted in various butterfly species. Body size differences have been observed in different ways, with owners being either larger or smaller than intruders, depending on the species (Hardy and Briffa 2013; Hernandez and Benson 1998). Flight muscle ratios and fat reserves also vary between species, with some exhibiting larger flight muscle ratios and larger fat reserves, suggesting different strategies in energetic contests (Peixoto and Benson 2011, 2012; Takeuchi 2006b, 2011). Additionally,

age differences between owners and intruders have been recorded, with older males investing more in current reproductive opportunities due to potentially fewer future chances (Kemp, 2000, 2003; Kemp *et al.*, 2006). Despite the presence of similar forms of aerial contests across different butterfly species, the characteristics correlated with ownership show significant variability.

Residency effect and experience on contest outcome

The intricate dynamics underlying territorial contests in butterfly species shed light on the pivotal role of residency asymmetry and experience in determining the outcomes of owner-intruder conflicts. In *Pararge aegeria*, conflicts of owner-intruder led to the consistent triumph of initial winners even when assuming the role of the intruder in successive contests. This phenomenon hints at the self-reinforcing nature of prior winning experiences, consolidating the dominance of aggressive resident males (Kemp and Wiklund, 2004). Similarly, experienced males of *Chrysozephyrus smaragdinus* regardless of physical attributes such as forewing length or age, demonstrated a heightened motivation to retain their territories, effectively maintaining their dominance over naive intruders. This tendency underscores the notion of subjective resource value, where residents, through their sustained investment in territory establishment and defense, accrue a higher pay-off, solidifying their position as the predominant beneficiaries in these territorial struggles. Such

findings prompt a deeper exploration into the intricate interplay between innate behaviour, prior experiences, and perceived resource value (Takeuchi, 2009).

Body size as a predictor of contest outcome

The importance of body size in determining success in physical contests within the animal kingdom is vividly exemplified by the case of the Satyrine butterfly, *Lethe diana*. Male butterflies engage in intense territorial disputes, employing linear chases and strategic monopolization of open spaces within the woods. It was observed that the male owners, those who consistently reclaimed territories, displayed a marked advantage in terms of body mass and larger body size is favored in such confrontations (Fig. 4A) (Takeuchi, 2011). Interestingly, a contrasting trend emerges in the nymphalid butterfly *Heliconius sara*, where smaller males are found to be more successful in defending mating arenas within the subtropical Brazilian forest (Fig. 4B). Males with shorter wing lengths enjoy longer territorial tenures, underlining the diverse dynamics at play in different species' competitive strategies (Hernandez and Benson, 1998).

Flight Muscle Ratio (FMR) as predictor of contest outcome

FMR, or flight metabolic rate, is a crucial determinant in the resolution of conflicts among male butterflies competing for territories. In *L. diana* owners with higher

FMR and higher body mass tend to dominate contests and superior flight performance correlates with ownership, emphasized by well-developed flight muscles in the owners (Fig. 5A) (Takeuchi, 2011). However, contests in *Hermeuptychia fallax* unveil a complex relationship between FMR, body mass, and contest outcomes. Males with higher body mass but lower FMR are more likely to emerge victorious in territorial contests (Fig. 5B) (Peixoto and Benson, 2012).

Body fat as a predictor of contest outcome

Fat reserves in *H. fallax* shed light on the significance of endurance in territorial disputes among males. Higher fat reserves and the predominance of males in the resident role suggest that endurance plays a critical role in determining the outcome of territorial conflicts (Peixoto and Benson, 2011). Conversely, in *C. smaragdinus* contest outcomes were negatively influenced by fat reserves. Residents exhibit lower fat content compared to intruders suggesting that the former consume more energy during territorial defence (Takeuchi, 2006). These insights collectively emphasize the intricate interplay between fat reserves, endurance, and territorial behaviour in the context of male residency status within these butterfly species.

Age as a predictor of contest outcome

The phenomenon of seasonal plasticity in body size is notably evident in *Hypolimnasbolina*, with older males

exhibiting a distinctive pattern of size fluctuation between autumn and spring. The seasonal dynamics of the contest outcome in this species seemed to be heavily influenced by age rather than size. Winners in spring were generally larger and older, whereas winners in autumn tended to be relatively smaller and older, suggesting that age served as the sole consistent predictor of contest outcome (Fig. 6A) (Kemp, 2000). Contrarily, the negative impact of age on contest outcome was also observed in *H. fallax*, younger males with greater residual fat content predominantly assumed the resident role, implying that the endurance of younger males was superior, potentially explaining their dominance in the resident position (Fig. 6B) (Peixoto and Benson, 2011).

Female motivates the losers

Interestingly, when loser males of *Pararge aegeria* were made to interact with females for 30 minutes, it resulted in a higher likelihood of winning subsequent contests against the original resident male in comparison, to the control group, spending the 30 minutes alone. In *P. aegeria*, the rate at which a resident male encounters other butterflies is a good indicator of the probability of also encountering receptive virgin females, *i.e.* a good predictor of territory quality (Bergman *et al.*, 2010).

Conclusions

In contests over territories, one male monopolizes a territory which is a mate-finding strategy where the probability of encountering a receptive female is high. Males visually detect passing females and pursue them for a mating chance, although females have no preference for these territories. Individuals win the contests because of differences in morphological or physiological traits and these traits vary widely among

species. In contrast with contests of other animals, where size and other morphological traits are usually correlated with RHP and can impose physical costs on their opponent, the ability to inflict physical costs on their opponent plays a minor role in butterfly contests. Apart from this motivation plays an important role in contest settlement like residency experience and interaction with females increases individual's motivation to fight and they stand to gain a higher pay-off in terms of mating chance.

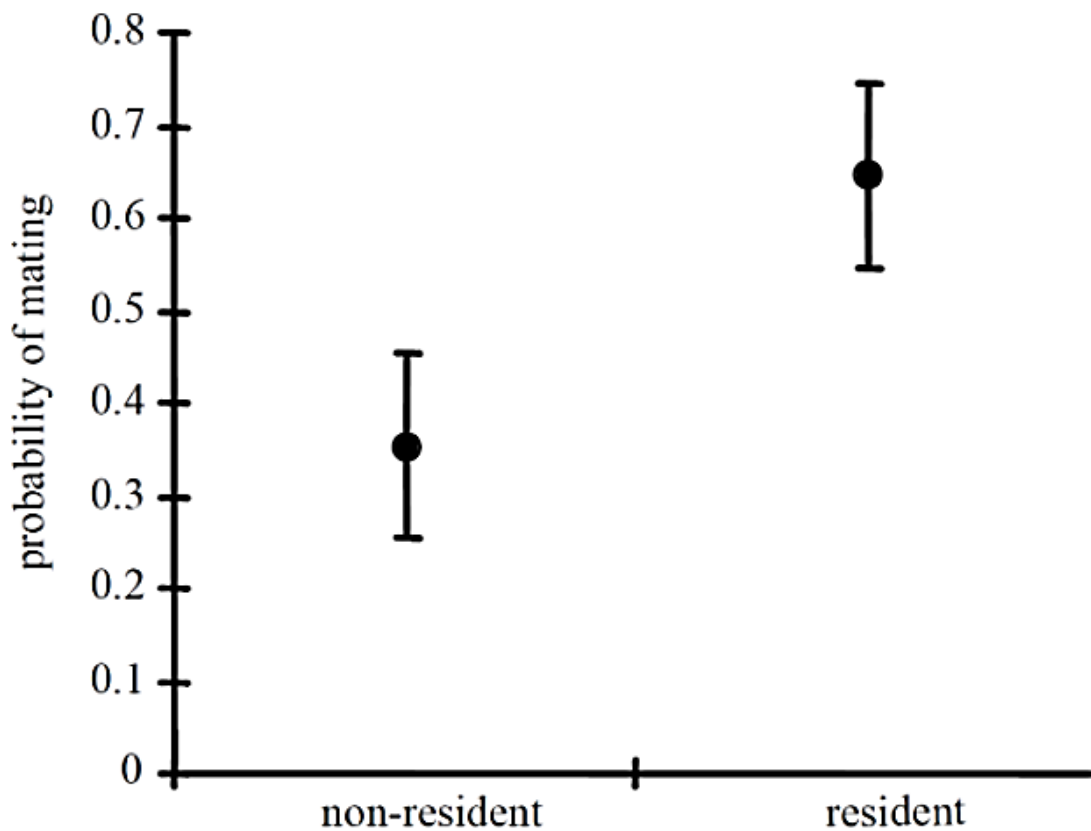


Fig. 1 Mating success of resident and non-resident males of *P. aegeria*.

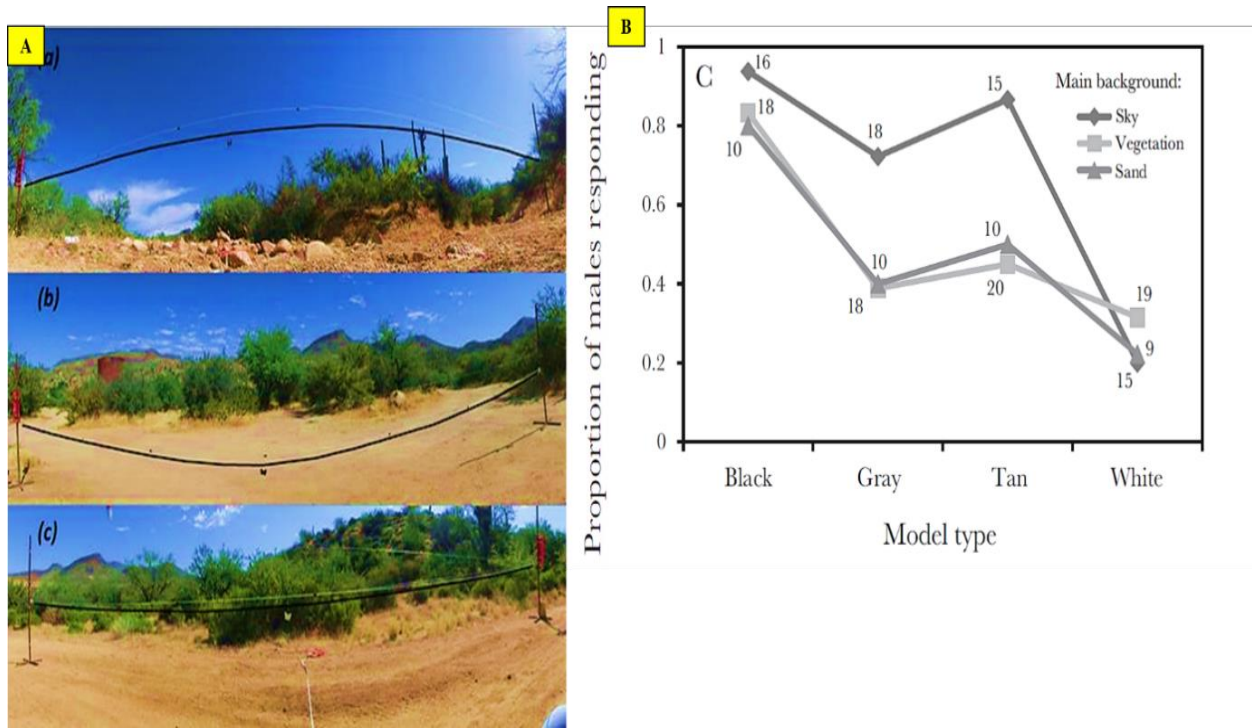


Fig. 2 A) Background classification images; B) The relationship between the proportion of perched males responding as a function of model and background type.

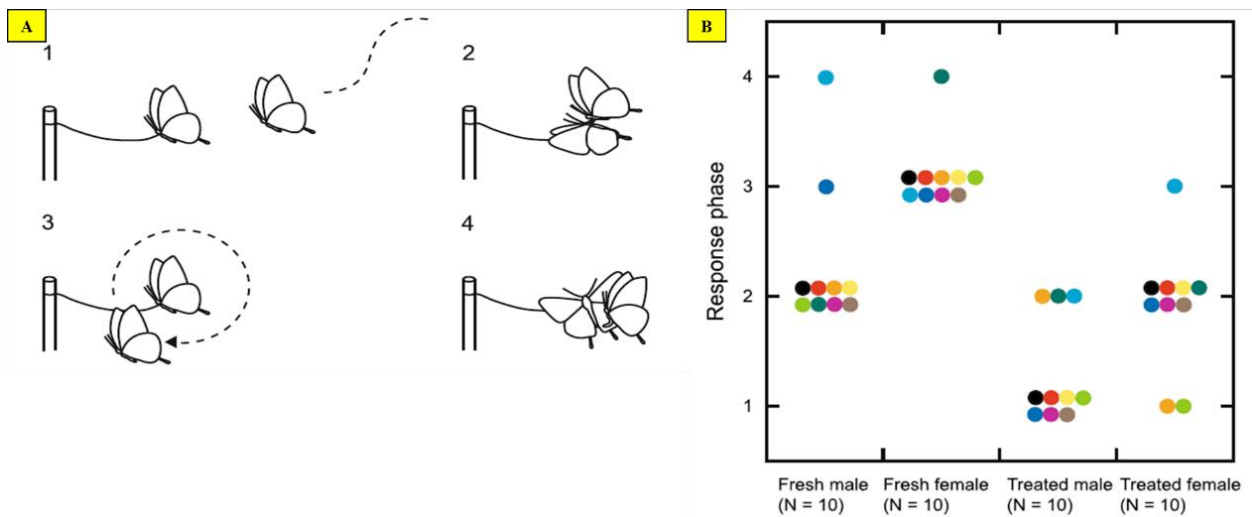


Fig. 3 A) Male response phases. 1. Approach; 2. Touch; 3. Courtship flight; 4. Copulation attempt B) Male responses to each specimen. Different colors indicate different individuals.

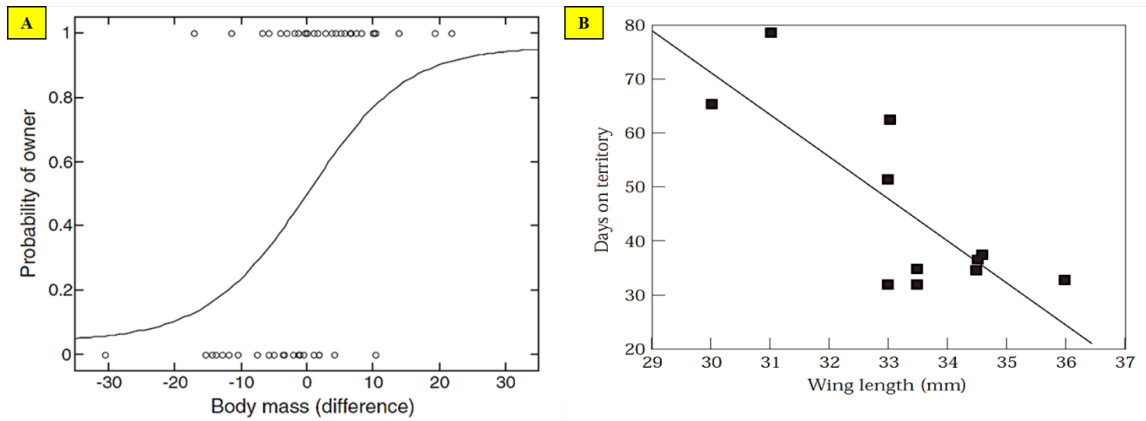


Fig. 4 A) Probability that the focal male was an owner as a function of body mass; B) Relationship between wing length and territorial time span (days).

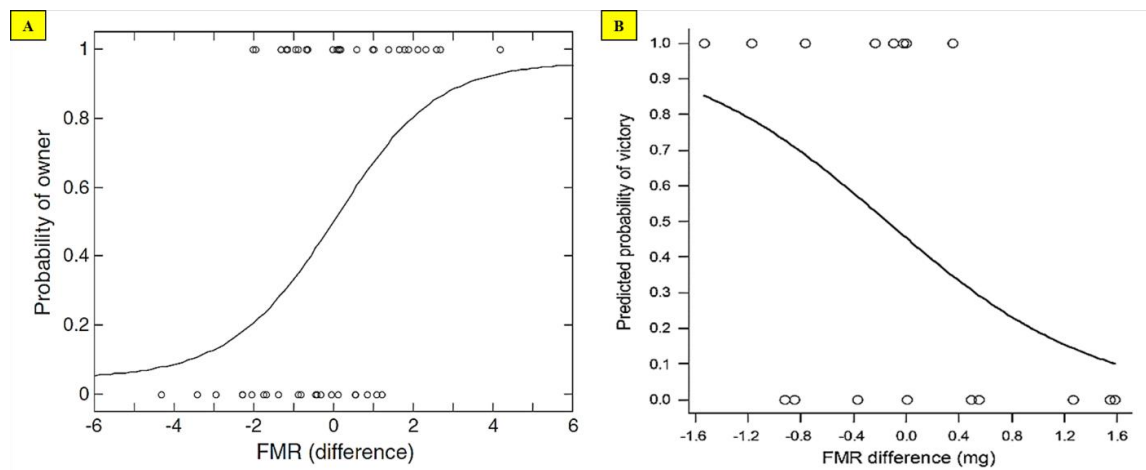


Fig. 5 A) Probability that the focal male was an owner as a function of the difference in FMR; B) Probability of victory of focal males of *H. fallax* in relation to FMR.

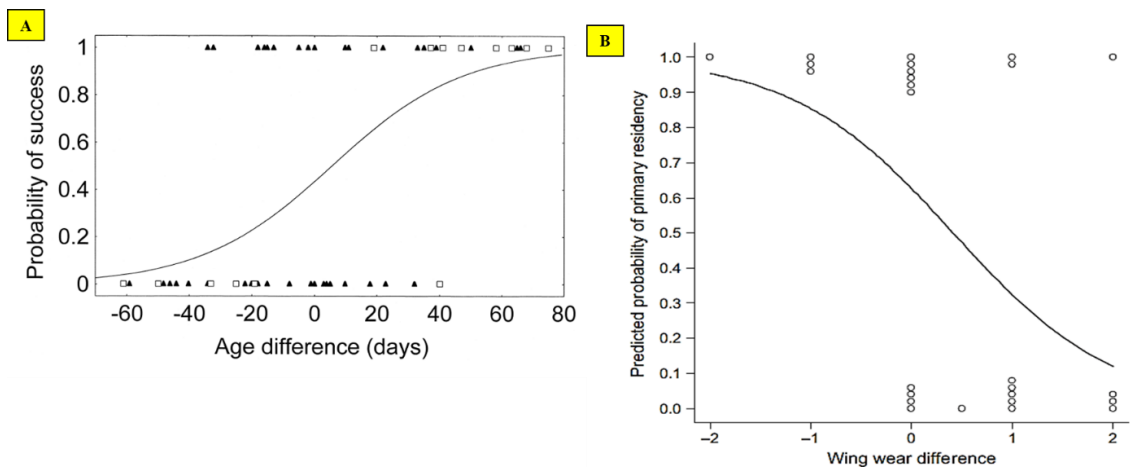


Fig. 6 A) Probability of success of focal males as a function of age in spring (squares) and autumn (triangles); B) Predicted probability of a male of *H. fallax* to be in the resident role in relation to the difference in wing wear.

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