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Slow wing flapping correlates with walking and flight preparation in puddling California tortoiseshell butterflies (*Nymphalis californica*)

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ABSTRACT

Besides flight, butterflies and moths utilize their wings for many processes, including thermoregulation, flight preparation, stabilization, olfaction, and anti-predator defense. California tortoiseshells (*Nymphalis californica*) flap their wings slowly when they puddle, but the reason why they do so is poorly understood. We constructed an ethogram of individual butterflies to determine whether slow wing flapping is a form of thermoregulation or caused by a behavioral mechanism. At a puddling site within Sagehen Creek Field Station, Northern California, we observed individual California tortoiseshell butterflies for five minutes, or until they flew away, whichever came first, noting initial time of day, shade level, and final ground surface temperature. In each 30-second interval, we counted the number of times the butterflies flapped their wings, and we noted whether they flew away or walked. Surface temperature and shade level had no effect on how frequently butterflies flapped their wings, but butterflies did flap more often later in the day. However, we found that California tortoiseshells flapped their wings more before they flew away, their flap rate increased when they walked, and they walked more later in the day. This suggests that flapping is not used for cooling, but instead may facilitate other behaviors, such as flight, walking, and olfaction.

Keywords: California tortoiseshell (*Nymphalis californica*), flapping, ethogram, puddling, butterfly

INTRODUCTION

Butterflies and moths (Lepidoptera) use their wings for various purposes other than flight, such as thermoregulation. Thermoregulation is one key process that wing posture and motion can regulate (Heinrich 1993; Tsai et al. 2020). When butterflies bask, dorsal baskers open their wings to reduce convective cooling (Wasserthal 1975; Heinrich 1993), and lateral baskers close their wings to conduct heat onto their thoraces (Kingsolver and Moffat 1982; Kingsolver 1985; Heinrich 1993). On the other hand, Tsai et al. (2020) found that papilionids flapped their wings after heating with a laser, presumably to cool down.

In addition to thermoregulation, lepidopterans flap their wings as part of other behaviors, including flight preparation, stabilization, olfaction, and anti-predator

defense. To increase wing muscle temperature for flight, red admirals (*Vanessa atalanta*) and oleander hawk moths (*Deilephila nerii*) vibrate their wings (Krogh and Zeuthen 1941; Dorsett 1962), and monarchs (*Danaus plexippus*) flap their wings (Kammer 1970). While this action influences temperature, we do not consider it as thermoregulation in our paper because it has a different ultimate purpose: enabling flight. Moreover, as small whites (*Pieris rapae*) walk across a vertical surface, they repeatedly flap their wings against the surface, improving their stability (Prisăcariu et al. 2026). Furthermore, some nocturnal moths flap their wings to better detect smells. When male silkworm moths (*Bombyx mori*) smell a female moth's pheromones, they fan their wings to increase the rate of air flow to their antennae, increasing the likelihood that they will detect more pheromones (Loudon and Koehl 2000). This fanning to induce air flow may apply similarly to the searching behavior of puddling butterflies, as they mainly rely on olfactory information to find puddling locations (Downes 1973). Additionally, wing flapping can be an effective anti-predator defense for butterflies and moths whose wings are cryptic on the ventral side and conspicuous on the dorsal side. In these species, wing flapping creates rapid color changes that, when combined with motion, may impede a predator's ability to locate prey (Murali 2018). Studying the contexts in which butterflies and moths flap their wings and why will provide insight into how they survive in their ecosystems.

Like many butterflies and moths, California tortoiseshells (*Nymphalis californica*) sometimes flap their wings while on the ground. California tortoiseshells' wings are orange with black spots on the dorsal side and mottled brown on the underside (Opler and Wright 1999), which may aid in camouflage (Scott 2020). They live in several western U.S. States, along with British Columbia and Alberta, Canada (Opler and Wright 1999). Like many butterflies and some moths, California tortoiseshells aggregate at mud puddles. This is part of puddling, a behavior in which insects drink nutrients that are low or absent in their diets, such as sodium and protein, from moist substrates like mud, dung, and carrion (Lamie et al. 2025). After butterflies puddle in one location for some time, they often move to a nearby location (Downes 1973), possibly because they have drunk all the nutrients in their original spot. Sometimes, California tortoiseshells flap their wings slowly as they puddle and as they walk, and there is variation in whether and how frequently they flap.

Although puddling has been researched extensively from a standpoint of resource acquisition and population dynamics (Lamie et al. 2025), there has been no study on why California tortoiseshells or other butterflies flap their wings while puddling. Several mechanisms might explain this flapping behavior. Since butterflies' wings heat up faster than their thoraces, California tortoiseshells may flap to cool their wings down like papilionids do (Tsai et al. 2020). Alternatively, they may flap their wings in conjunction with other behaviors, such as flight or walking. Like how red admirals, oleander hawk moths, and monarchs warm up their wing muscles with vibrations or low-amplitude flaps (Krogh and Zeuthen 1941; Dorsett 1962; Kammer 1970), California tortoiseshells may prepare for flight with high-amplitude flaps. Furthermore, because nymphalids have reduced, non-functional front legs (Opler and Wright 1999), they may

walk unstably (Full and Tu 1990). It is possible that, like how small whites flap their wings for stability when walking on vertical surfaces (Prisăcariu et al. 2026), California tortoiseshells may flap their wings while walking to keep their balance. If this were the case, then we might also expect them to flap their wings more later in the day, when they may need to walk further to locate remaining nutrients in the puddles (Downes 1973). Moreover, they may also flap their wings to funnel odorants towards their chemoreceptors as silkworm moths do (Loudon and Koehl 2000), helping them locate desirable nutrients in the puddles.

We constructed an ethogram, investigating why California tortoiseshells flap their wings as they puddle. First, we hypothesized that, if California tortoiseshells flap their wings as a form of cooling, then they will flap more frequently at higher temperatures, in direct sunlight, and later in the day, when temperatures are typically warmer. Second, we expected two behavioral patterns: (a) if they flap their wings for flight preparation, then they will flap more before flying away; and (b) if wing flapping improves their stability, then they will flap more frequently when walking than when they are stationary. Lastly, we predicted that butterflies would walk more later in the day, possibly as nutrients became locally depleted.

METHODS

2.1 Study Site and Natural History

All research was conducted at Sagehen Creek Field Station on August 1 and 2, 2026, in Nevada County, California. The reserve (39.431847, -120.240710; 1941.4 m elevation) is approximately 16 km north of Truckee, California, and it sits in the 3,642-hectare Sagehen Experimental Forest (U.S. Forest Service 2025). The forest has a Mediterranean climate, with mean maximum temperatures ranging from 4 °C in December to 26 °C in July. Precipitation averages roughly 850 mm of rain and 5000 mm of snow each year. The forest is dominated by pines (*Pinus* spp.) and firs (*Abies* spp.), and understory shrubs include *Ceanothus* spp. and greenleaf manzanita (*Arctostaphylos patula*) (U.S. Forest Service 2025). The montane meadows are dominated by various grasses and sparse ranger's buttons (*Angelica capitellata*).

Our study site was made up of three adjacent puddles (puddles 1, 2, and 3) along Sage Hen Road (puddles centered around 39.433105, -120.247763; 1957.5 m elevation). The dirt road cuts through the upstream end of a wet montane meadow, the water in which comes from a tributary of Sagehen Creek. Puddle 1 had the largest standing body of water and was directly fed by the tributary; a thin layer of duff covered the wet ground nearby. Butterflies puddled the most at puddle 1 and the least at puddle 2. Puddle 3 was surrounded by cobbles and did not have standing water. Various species visited the puddles, including a great basin fritillary (*Speyeria egleis*), a Lorquin's admiral (*Limenitis lorquini*), a mourning cloak (*Nymphalis antiopa*), wasps (family Sphecidae), flies (order Diptera), red crossbills (*Loxia curvirostra*), and squirrels and chipmunks (family Sciuridae). Most California tortoiseshells puddled between 10:00 am and 5:00 pm, and they did not seem disturbed by the other species.

California tortoiseshells live in brush habitats and open forests, and males exhibit hilltopping behaviors (Opler and Wright 1999). Adult California tortoiseshells emerge in late June, and they live until the next April

or May. In autumn, these butterflies migrate southwest from high-altitude regions like the Sierra Nevada to their habitats in the Coast Ranges and lower elevations for overwintering, and they return northeast in spring (Scott 2020; Shapiro 1975). They experience population booms every five to thirteen years, reaching millions in some areas (Shapiro 1975; Powell 1972). The adults drink nectar from small, pale-colored flowers like those of *Ceanothus* and *Arctostaphylos* as well as exudates on various conifers (Caldwell 2017; Valenti et al. 1997). The larvae live on and eat *Ceanothus* spp. as host plants.

2.2 Research Design

We opportunistically sampled California tortoiseshells at the puddles between 9:30 am and 5:30 pm on both days. Because most butterflies were in full sunlight, we target-sampled for those in shade to better compare behaviors in sun versus in shade. We classified a butterfly's location as shade if the butterfly stood directly or partially in shadow or if they were less than a body length away from shadow to account for shadows moving. We observed that we could watch the butterflies closely without disturbing their behavior as long as we stayed still, so we did not set a minimum distance for observations.

For each butterfly, we first recorded the shade level and the start time of a five-minute observation period. In each 30-second block, we counted how many times the butterfly flapped, which we defined as them moving their wings down and up by more than 10° based on a visual estimate, and we recorded whether they flew away or walked (took at least one step in any direction). After five minutes, we measured the surface temperature underneath the butterfly's ending point with an Etekcity lasergrip 774 infrared thermometer. We then selected another butterfly and repeated this process. Because we could not mark or otherwise identify individual butterflies, we could not confirm each measurement was of a unique individual.

2.3 Statistical Analyses

We conducted statistical analyses in JMP (2026 JMP® Version 18. JMP Statistical Discovery LLC, Cary, NC.). In the linear regression and the t-tests, we took the natural logarithm of the flap rate (flaps per minute) data to obtain a normal distribution. For environmental factors, we examined the relationship between flap rate and surface temperature with a linear regression. Then, we ran a t-test comparing the flap rate between butterflies in direct sunlight and butterflies in shade. We also calculated the Spearman rank correlation coefficient between flap rate and the time at which we started observing a butterfly, for we could not attain a normal distribution by taking the natural logarithm of the time data. For behavioral factors, we first ran a Mann Whitney U test to determine whether the number of flaps during the last full 30 seconds of observation, which were non-normal, differed between butterflies who flew away during the five-minute observation period and those who did not. If a butterfly flew away at the 2:12 time mark, for example, we would use how many flaps they made in the 1:30–2:00 interval. Additionally, we compared the flap rates between butterflies who walked and butterflies who stood still with a t-test. Finally, we calculated the Spearman rank correlation coefficient between how often a

butterfly walked and the time when we started observing them.

RESULTS

We gathered data on 121 California tortoiseshell butterflies. The mean flap rate was 11.41 flaps per minute, and the median was 10 flaps per minute. We measured the surface temperature near 68 of the butterflies, and we recorded shade level for 119 of them.

Even though the surface temperature varied from 17.5 °C to 43.5 °C over the study, there was no relationship between flap rate and surface temperature ($N = 68$, $R^2 = 0.0011$, $p = 0.79$). Similarly, we found no difference in flap rate between butterflies in full sun and butterflies in shade ($N_{Full\ Sun} = 63$, $N_{Shade} = 56$, $t = 0.27$, $p = 0.81$). However, butterflies who we observed later in the day tended to flap their wings more frequently ($N = 121$, $\rho = 0.19$, $p = 0.038$; Fig. 1).

Butterflies who flew away during the five-minute observation period flapped their wings more during the last full 30 seconds of observation than butterflies who stayed throughout the five-minute period ($N_{No} = 71$, $N_{Yes} = 50$, $Z = 3.38$, $p = 0.0007$; Fig. 2). In addition, butterflies who walked at least once flapped more often than those who did not ($N_{Stayed\ Still} = 34$, $N_{Walked} = 87$, $t = 1.07$, $p = 0.0003$; Fig. 3). Finally, California tortoiseshells who we observed later in the day tended to walk more ($N = 121$, $\rho = 0.37$, $p < 0.0001$; Fig. 4).

DISCUSSION

Overall, our findings indicate that California tortoiseshells' flapping is influenced more by behavior than by environment. We hypothesized that, if California tortoiseshells flap their wings for cooling, then they would flap their wings more often at higher surface temperatures and in sunlight. Neither of these predictions were supported by our data. Though, since we do not know the thermal tolerances of the California tortoiseshell butterflies, it should not be assumed that these butterflies do not have thermoregulatory cooling behaviors. It is possible that, like what Tsai et al. (2020) found after heating papilionids' wings with a laser, California tortoiseshells may flap their wings to cool them off under high heat stress. Kemp and Krockenberger (2002) found that butterflies shelter from stressfully high temperatures in shade, yet most of our butterflies were in the sun. We even saw some butterflies basking with their wings fully open, which is a warming behavior (Heinrich 1993). A future study could determine the thermal limits of the California tortoiseshell, which could inform further research about their thermoregulation.

Our second prediction, that wing flap rate would be correlated with their flight and walking behaviors, was fully supported by our findings. California tortoiseshell butterflies flapped their wings more often shortly before flying away or while walking compared to when they were stationary. These patterns suggest that California tortoiseshells may flap their wings for flight preparation and ground locomotion.

Wing flapping may warm up California tortoiseshells' flight muscles before takeoff, contributing to flight preparation. Some wing motions are known to increase thoracic temperature to aid in flight (Krogh and Zeuthen 1941; Dorsett 1962; Kammer 1970). Butterflies and moths cannot fly if their thoracic temperatures are too low (Dorsett 1962; Kammer 1970). We saw that California

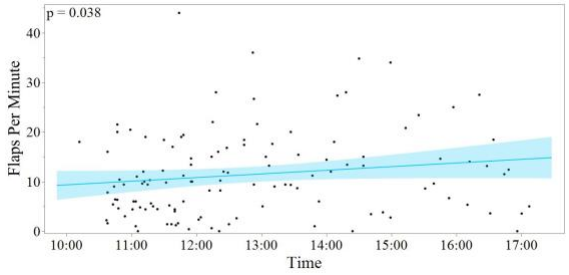


Figure 1. California tortoiseshells (*Nymphalis californica*) who were observed later in the day flapped their wings more often. Data were collected at Sagehen Creek Field Station, Nevada County, California, on August 1-2, 2026. (N = 121, ρ = 0.19, p = 0.038).

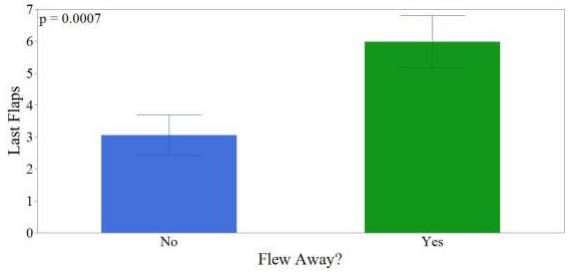


Figure 2. California tortoiseshells (*Nymphalis californica*) who flew away during a five-minute observation period flapped their wings more in the last full 30 seconds of observation than California tortoiseshells who did not fly away. Data were collected at Sagehen Creek Field Station, Nevada County, California, on August 1–2, 2026. Each error bar was created with one standard error from the mean. (N_{No} = 71, N_{Yes} = 50, Z = 3.38, p = 0.0007).

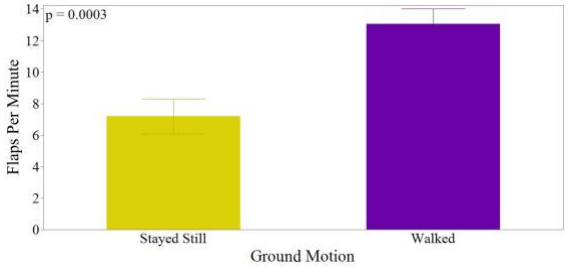


Figure 3. California tortoiseshells (*Nymphalis californica*) who walked flapped their wings more often than those who stayed still. Data were collected at Sagehen Creek Field Station, Nevada County, California, on August 1–2, 2026. Each error bar was created with one standard error from the mean. ($N_{Stayed\ Still}$ = 34, N_{Walked} = 87, t = 1.07, p = 0.0003).

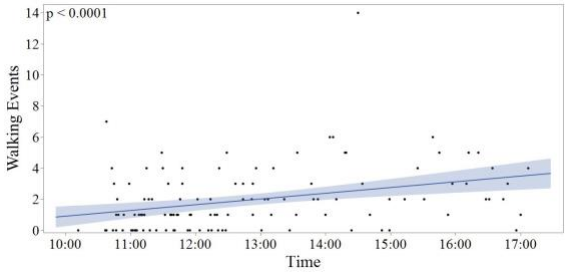


Figure 4. California tortoiseshells (*Nymphalis californica*) walked more later in the day. Data were collected at Sagehen Creek Field Station, Nevada County, California, on August 1–2, 2026. (N = 121, ρ = 0.37, p < 0.0001).

We saw that California tortoiseshells flapped their wings more right before flight, which supports our hypothesis that wing flapping may be a form of flight preparation. However, the behaviors known to increase thoracic temperatures in butterflies and moths are vibrations or low-amplitude flaps, but our behavior of interest was slow, high-amplitude flaps. Also, we had no way of measuring the thoracic temperature of our butterflies, so we cannot determine whether an internal temperature increase was the mechanism behind our findings (Krogh and Zeuthen 1941; Dorsett 1962; Kammer 1970). Measuring California tortoiseshells' thoracic temperatures as they flap may elucidate the relationship between flapping on the ground and flight in this species.

Also, a possible explanation for why California tortoiseshells flapped more when they walked is that flapping provides stability. Nymphalids only use their middle and hind pairs of legs for walking (Opler and Wright 1999), which is inherently unstable compared to how most other insects walk with all six legs (Full and Tu 1990). We thought that flapping might aid California tortoiseshells in locomotion by providing

stability. It might be similar to how small whites flap their wings vigorously while standing or walking on a vertical surface, applying a normal force that prevents them from falling (Prisăcariu et al. 2026). However, the wingbeat frequencies observed by Prisăcariu et al. (2026) were much higher than those of our puddling butterflies. It seems that wings have to be beating at near flight speed to stabilize a butterfly, at least on a vertical surface. It seems unlikely that the slow wing flapping of a walking California tortoiseshell butterfly is associated with their stability, but more research is needed to determine whether slow flapping can aid in balance on a horizontal surface.

Furthermore, California tortoiseshells may also flap their wings while walking to enhance olfaction in their search for nutrients. Downes (1973) noted that butterflies find puddling locations through smell but specific drinking spots with seemingly random walking; it is possible, though, that olfaction may also play a role in the latter process. We propose that, to aid in locating drinking spots, California tortoiseshells may flap their wings to bring more olfactants to their antennae. This might be similar to how moths flap their wings rapidly to increase air flow through their antennae, replacing pheromone molecules that they have already taken up (Loudon and Koehl 2000; Baker and Cardé 1979). However, the wingbeat frequencies observed by Loudon and Koehl (2000) and Baker and Cardé (1979) were near flight frequency—much faster than our observed wing flaps. The wing flapping of walking California tortoiseshells may be too slow to aid olfaction in this way. In addition, butterflies are known to sense chemicals with their feet (Chun and Schoonhoven 1973; Minnich 1921), so even a marginal boost in smell from slow wing flapping is unlikely. Moreover, we do not know what nutrients the California tortoiseshell butterflies are acquiring from puddling. Our pilot study on their nutrient preference proved to be unsuccessful; the butterflies ignored all of our nutrient treatments, both in situ and in captivity. Perhaps a future study with a different species could measure wing flap frequency on butterflies puddling on mud with various concentrations of their desired nutrients.

Additionally, California tortoiseshells may also flap their wings while walking as an anti-predator defense. Camouflage is an effective measure against predation among insects (de Alcantara Viana et al. 2022). However, movement breaks the efficacy of camouflage—the instant a camouflaged animal moves, they become more visible to predators (Tan et al. 2024). This is not ideal for a California tortoiseshell butterfly walking to a nearby drinking spot. However, this can be counteracted. A camouflaged animal is much harder to track and be pecked by birds if they flash bright colors while they move (Murali 2018; Pike 2015; Murali et al. 2019). The ventral surfaces of California tortoiseshells' wings look similar to rocks near a creek, which may make the butterflies well-camouflaged (Scott 2020). The dorsal surfaces of the wings, however, are a bright orange. The rapid color change that occurs when the butterfly flaps may be an anti-predator measure, reducing the likelihood of a successful predator attack (Murali 2018). However, we saw no common ravens (*Corvus corax*), who are predators of California tortoiseshells (Hendricks 2005), near the puddles, and the red crossbills did not seem interested in them at all. Future researchers could conduct experiments with

common ravens and California tortoiseshell models that simulate wing flaps and walking to investigate whether the combination of these behaviors impedes predator attacks.

Finally, we found that California tortoiseshells walked more later in the day. While we originally predicted that this would hold true due to thermoregulation, since walking also increased later in the day, it may be driven by puddle dynamics. Downes (1973) observed that butterflies walk randomly until a desirable drinking spot is found, but it is quite possible that they use their chemoreceptors to locate drinking spots. As more California tortoiseshells drink from the puddles, the desired nutrients may become more depleted, and they may have to walk farther to find an adequate drinking spot. As these puddles are fed by a tributary to Sagehen Creek, we assume the nutrients may be replenished, though not faster than the butterflies uptake them during the day—the nutrients are fully replenished after the butterflies leave.

In summary, it is unlikely that California tortoiseshells flap their wings while puddling for thermoregulation, but this behavior is likely tied to their flight and walking behaviors. They may flap their wings more before flying if the flapping prepares them for flight. Also, they may flap while walking for stability, olfaction, or defense against predators. However, more research is needed to determine which of these mechanisms, if any, explain the patterns we observed. This study and future studies may provide a framework for other researchers in investigating how butterflies and moths utilize their wings to survive.

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