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Authors
Strong, Donald R
John, Christian

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ORIGINAL ARTICLE

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Moisture and distribution of a keratophagous moth, *Tinea occidentella*

Donald R. Strong[1] | Christian John[2]

[1]Department of Evolution and Ecology and Bodega Marine Laboratory, University of California, Davis, California, USA

[2]Department of Wildlife, Fish, and Conservation Biology, University of California, Davis, California, USA

Correspondence
Donald R. Strong, Department of Evolution and Ecology and Bodega Marine Laboratory, University of California, Davis, CA 95616, USA.
Email: drstrong@ucdavis.edu

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Abstract

1. Keratophagous insects consume proteinaceous foods (animal hair, feathers, and other substances containing keratin) that are low or even lacking in water, which necessitates a source of moisture beyond the primary diet.
2. *Tinea occidentella* Chambers 1880 (Lepidoptera, Tineidae), which feeds upon the keratin in fur and feathers in mammalian carnivore scat and in pellets of birds of prey (foods very low in water), affords an understanding of the ecology of keratophagous insects in nature. The common name "western clothes moth" is a misnomer as it does not eat clothes but only scat and pellets.
3. In laboratory experiments, we found that larvae did not absorb water vapour directly from the atmosphere, and they died at 45% rh–55% relative humidity (rh). We found no evidence that larvae drank. Larvae grew normally, had high survival, pupation, and eclosion only when feeding at very high (>88%–99%) rh upon fur from pellets and scat; the fur absorbed water from the atmosphere.
4. While scat and pellets are abundant throughout North America, *T. occidentella* is mostly restricted to the moist, mild climates of coastal central and southern California, where fog, dew, and morning high rh of 99% are common. Outside of this coastal envelope where growing season climate is warmer, drier, and becoming more so, the species is rare.
5. An intriguing notion, requiring research beyond the present report, is that the warming and drying climate of southwestern North America will contract the range of this insect.

KEYWORDS
distribution, fog, keratophage, moisture, moth, pellets, scat

INTRODUCTION

Keratophagous arthropods include Lepidoptera (Braack, 1987; Lee et al., 2020; Robinson & Nielsen, 1993) and Coleoptera (Scholtz, 1986) that are distributed over all continents except Antarctica. Although larvae of most Lepidoptera and many Coleoptera find abundant water in their plant-based diet (Ramsay, 1976), keratophages can develop with little or no free water in their primary nutrient. Our research concerns a microlepidopteran species *Tinea occidentella* (Tineidae) with larvae that feed only on the keratin in undigested fur and feathers eliminated by coyotes, bobcats, and mountain lions, birds of prey, and vultures (Strong, 2018).

Multiple species of keratophagous insects feed upon the variety of keratin sources in bird nests (Barton & Bump, 2019) and necrophagous beetles feed upon desiccated animal carcasses rich in keratin (Scholtz, 1986). Insect keratophages are an important component of communities of carrion decomposers (Chown et al., 2011). Dermestid beetles feeding in bird nests, characterised by the genus *Anthrenus*, are mainly

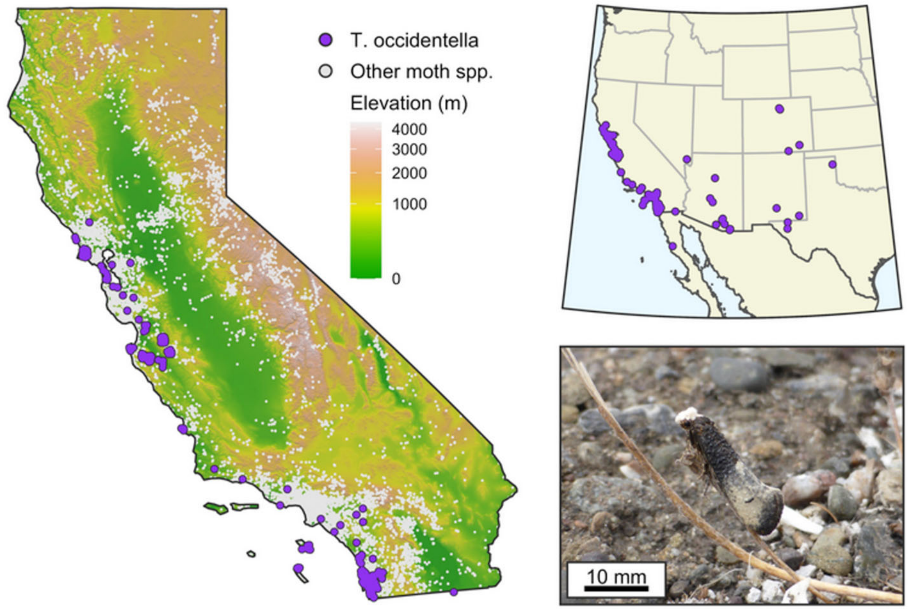

FIGURE 1 *Tinea occidentella*, lower right. Map (left) of California with elevations. Locations from museum records of the California of *Tinea occidentella* shown as violet dots (Appendix A.3) and locations of the 24,099 observations of 713 other moth species as grey dots, known from the state of California (GBIF.org [28 July, 2021] GBIF Occurrence Download, 10.15468/dl.j765xk). Map (upper right), *T. occidentella* range in the United States; see also Appendix A.3.

keratophagous and ingest food of less than 12% relative humidity (rh), while those of the genus *Desmestes* feed mainly upon the soft tissues of carcasses with greater than 15% rh and take the tougher keratinaceous tissues as a minor component of their diet (Zhantiev, 2009).

Lepidopteran keratophages include notorious domestic pests, the multiple species of clothes moths (also in the genus *Tinea*), with larvae that feed upon silk, spider webs, lint, leather, feathers, wool, and animal hair, among other items (Nasu et al., 2012). Larval silk spinning is a key adaptation of Lepidoptera that prevents desiccation in caterpillars (Marquis et al., 2019; Wagner & Hoyt, in press), and the role of silk for keratophages in this order is prominent. The larvae of domestic-pest clothes moth *Tinea pellionella* spend their entire lives within a silk cocoon that absorbs water (Plarre & Krüger-Carstensen, 2011), and without the cocoon the larvae lose body water rapidly (Chauvin et al., 1979). Reminiscent of, and closely related to, *T. occidentella*, the silk tubes of *Ceratophaga vicinella* (Tineidae) are spun by larvae that feed upon the keratin plates of dead gopher tortoise shells; as in *T. occidentella* the larval tubes extend down into the sand (Deyrup et al., 2005). The larvae of another close relative to *T. occidentella*, *Ceratophaga vastella*, live within tunnels of silk and feed upon the horns of dead ungulates in tropical Africa (Braack, 1987). Geography gives these species high rh and a mild climate. *C. vicinella* lives in central Florida with high humidity, frequent summer rains, and only very rare freezing temperatures (Archbold Biological Station, Research, Conservation and Education, 2021). The tropical African environment of *C. vastella* larvae spans the equator, has high rh, year-round mild temperatures between 15° C and 28° C, and rainfall year-round (Serengeti Weather & Climate Chart, 2021).

The reported adaptations of arthropods challenged by low moisture are retention of water by the gut and integument, drinking water, oxidising food to produce metabolic water, and absorbing water vapour directly from the atmosphere in osmotically specialised buccal and rectal tissues (Chown & Nicolson, 2004). Our experiments cast doubt on all of these but retention of water by the gut and integument for *T. occidentella*. We discovered an additional adaptation with which *T. occidentella* met the water challenge of keratophagy. The species is mostly restricted to the mild, humid climates of coastal California, where advective fog commonly forms dew and morning rh of 99%. We found that successful development is achieved by consumption of fur and feathers that have absorbed moisture from an atmosphere of high relative humidity (rh). Speculating about linking these insights to the distribution of this insect, the climate change that is warming and drying southwestern North America could be shrinking the range of this insect. Future research will be necessary to test this speculation.

METHODS

Our first objective was to observe *T. occidentella* adults (Figure 1, lower right) and larvae in the laboratory (Figure 2a,b) and in the field in pellets (Figure 2c), and in scat (Figure 2d,e,f). In the field, we captured adults in funnel traps baited with coyote scat and owl pellets and recorded moths with time lapse photography focused upon groups of scat and pellets. We used fresh scat and raptor pellets collected at the Bodega Marine Reserve of the University of California, Davis (BMR, https://marinescience.ucdavis.edu/bml/bmr) and owl pellets collected at roosts in Davis CA and purchased mainly from Lisa and Ethan Li (2334 W. Jayton Dr., Meridian, Idaho 83,642, USA, email

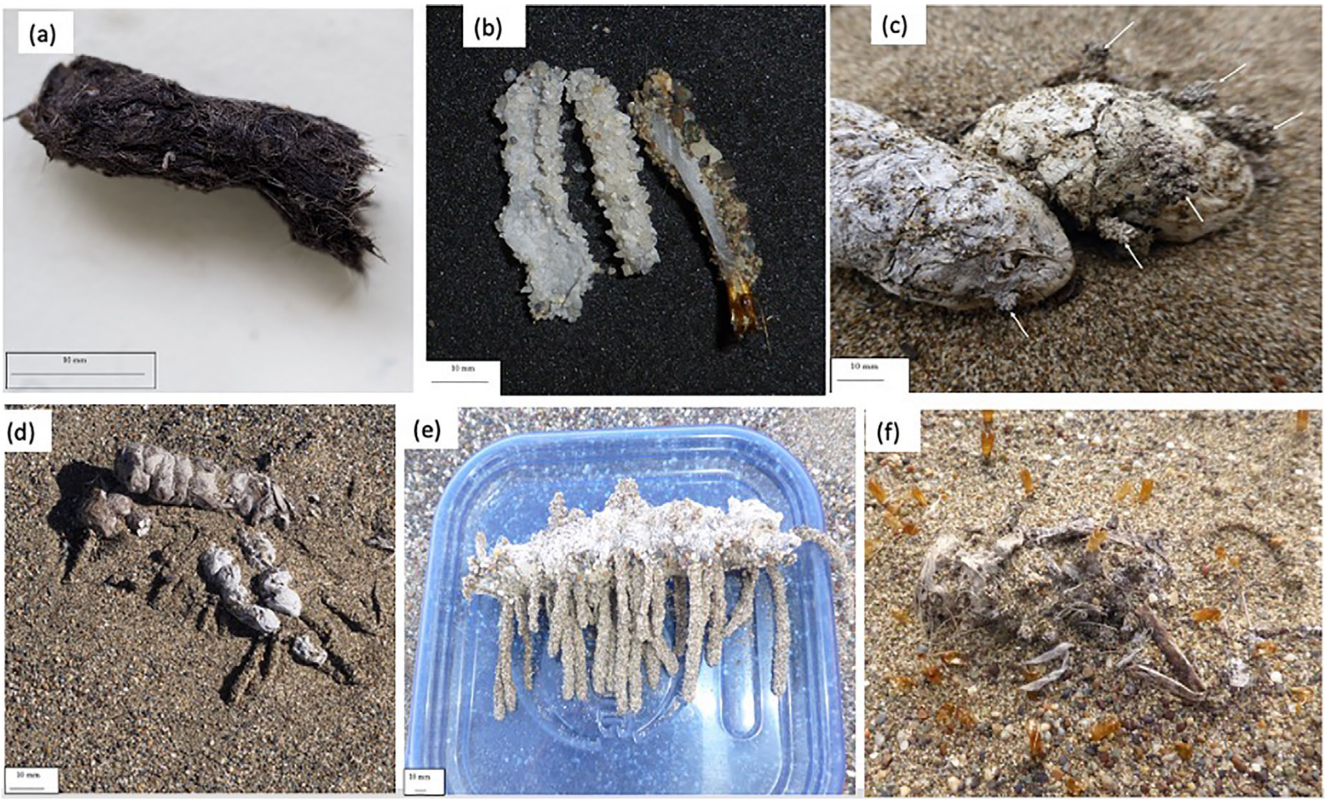

FIGURE 2 (a) Larval *Tenia occidentella* on experimental pellet of prey fur extracted from owl pellet. The moth had laid an egg into the pellet ca. 5 days before the photo. (b)–(f) Silk tubes spun by *T. occidentella*. The tubes were adhesive and collected frass and sand on their exteriors. (b) Tubes covered with sand. Tube on the left has been cut open. The tube and pupal shell on the right were made during development by the larva in (a). The pupal shell, from which the moth eclosed, protrudes, from the tube on the left. (c) Silk tubes of small larvae (white arrows) beginning to protrude from owl pellet. These emerging tubes were covered with frass produced by the larva. Each tube was used by a single larva. (e) Tubes from scat that extended downward into the sand (the scat and tubes were laid on their side for the photo). Tubes penetrated to depths of ca. 5 cm where the sand was moist and midday temperatures on clear days were much lower (≈10°C) than at the surface of the sand (≥40°C). (f) (amber) pupal shells protruding from the ends of silk tubes, each of which had yielded a moth.

address, lisanadam@gmail.com). These sources of owl pellets are far from recorded localities of *T. occidentella*. We made funnel traps from 1 litre, plastic, soft drink bottles by inverting the cut-off top into the remaining part of the bottle.

Our second objective was to understand the oviposition, growth, and development of larvae. We obtained larvae for laboratory experiments from scat and from owl pellets that we found or placed in the field. We obtained eggs in the laboratory by allowing moths to oviposit in small experimental pellets made from the fur in owl pellets. First instar larvae hatched from these eggs. Larvae were reared to maturity on scat and owl pellets. We performed laboratory experiments with treatments of moisture and food. For multiple treatments (Figure 3a,b, Appendix A.1 and A.2) we ranked larvae by weight then assigned each to treatments sequentially from the ranking. Thus, for three treatments, the least massive larva was assigned to treatment a, the second least to treatment b, the third to treatment c, the fourth to treatment a, and so on. Phagostimulation and growth experiments were done with sheep wool soaked in liquid made by placing owl pellets and coyote scat in water.

We weighed larvae of *Tinea occidentella* and other things for this study on a Mettler XS205 balance that displayed mass to 0.01 mg. Scat, pellets, and larvae were maintained at 99% rh prior to laboratory experiments. For the moisture and feeding experiments we held individual larvae in plastic 30 mm × 15 mm petri plates, kept within larger sealed plastic boxes.

The mean ambient rh of the laboratory during the experiments was ca. 45% (min. = 35% rh, max. = 55% rh). We regulated rh for experiments in plastic boxes with lids. We made rh lower than ambient by covering the bottom of boxes with silica gel and placing the petri plates containing larvae on top of a screen over the silica gel. We elevated rh by placing sponges soaked in water on the bottom of the boxes and placing the petri plates containing larvae on top of a screen over the sponges. We set values of rh by varying the number and sizes of holes in the lids of the boxes. The lowest rh was in boxes with silica gel and small holes. Higher rh than ambient was made in boxes with sponges and small holes in the top of the box. We measured rh with data loggers placed among the petri plates containing the larvae in the boxes (Minnow Temperature and Humidity Data Logger TM, Senonics). The data loggers showed that rh changed from ambient to

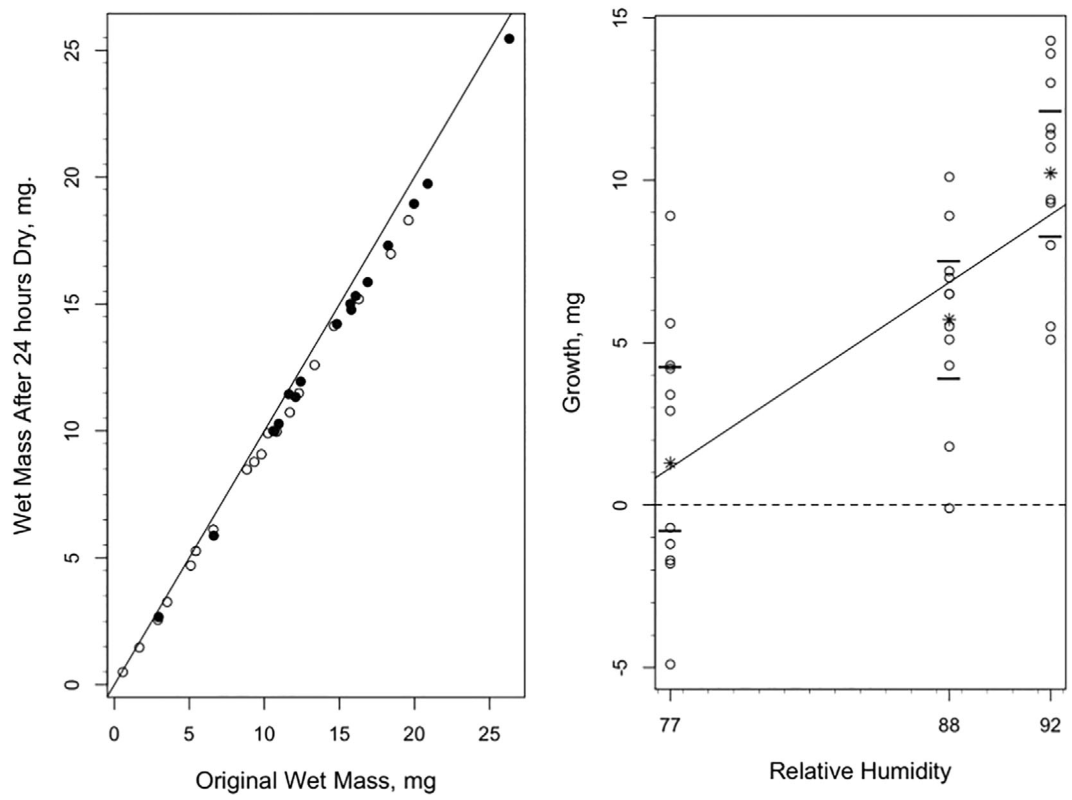

FIGURE 3 (a) Y axis, larval mass of *Tinea occidentella* larvae after 24 h at 70% rh. X axis, original larval mass when removed from silk tube after at least one week at 99% rh. Solid points indicate the 16 larvae that spun silk tubes during the 24 h at 70% rh. Open points indicate larvae that did not spin silk tubes during the 24 h at 70% rh. (b) Growth in mg of intermediate-sized of *Tinea occidentella* larvae as a function of relative humidity. Mean mass (stars) in mg increased over these three values of rh as shown by the regression, Growth = 1.5 rh-3.9. p intercept = 5.1e-05, p slope = 6.3e-06. Horizontal bars encompass the standard error of the mean for each rh category. Growth in mg at each rh. 77% rh: mean (sem) = 1.7 (1.3), median = 3.9, maximum = 8.9. 88% rh: mean (sem) = 5.7 (0.9), median = 6.5, maximum = 10.1. 92% rh: mean (sem) = 10.2 (1.0), median = 11.0, maximum = 14.3.

the desired values within a few hours after the boxes were closed, and the desired rh value was maintained within 2% for the duration of the experiments.

Our third objective was to examine the broader distribution of *T. occidentella* (Figure 1, left and upper right). The points on these maps include iNaturalist records and museum records with latitude and longitude (Appendix A.3). We learned the temperature and rh of where the insect lives in California from (Shideler, 2021; Dendra, 2021; temperature and humidity where it has not been reported in California were from CIMIS, 2021).

RESULTS

Phenology and field behaviour

Tinea occidentella Chambers is a large microlepidopteran (Figure 1, lower right) described in 1880 and known from the coast of central and southern California (Powell & Opler, 2009, Figure 1, left). In this coastal envelope the maritime influence produces advective fog, dew, and very high rh; this mild coastal climate also lacks hard freezes and high summer temperatures. Mornings along the central and southern California coast were often foggy with dew that wetted coyote scat, owl pellets, the ground, and the vegetation throughout the year (DRS personal observation, 2017–2022). In contrast, the white dots in Figure 1, upper left show the recorded locations of other species of moths over the entirety of California, which by and large lacks the mild climate of the coast.

We observed growth, manifested by elongation of silk tubes spun by larvae onto and into the sand from March through October at BMR. In July and August most scat and owl pellets contained larvae of *T. occidentella*. From November to March elongation of silk tubes slowed, and appearance of pupae ceased. Scat and pellets placed on the sand at BMR in the first week in June produced pupae at the end of September, within ≈70 days, and moths within ≈80 days.

During the March – October growing season of *T. occidentella*, maximum daily relative humidity (rh) at BMR was less than 80% only 4% of days and less than 90% rh only 16% of days; rain was infrequent and occurred mainly during March in most years, 2017–2021 (Shideler, 2021). Lower rh was more frequent during the winter months when larval growth was nil. The maximum rh was <80% 15%

of days and < 90% 31% of days during November – February of these years. Most rain fell in winter.

The daily mean air temperature at BMR in the growing season, 2017–2021 was 12.3°C, and the minimum was 7.3°C. The maximum daily mean air temperature of 21.3° was unusual. Only 7% of days during the growing season, 2017–2021, had mean temperature ≥15°C (Shideler, 2021). During November–February mean air temperature was 10.7 C (minimum = 1.56, maximum = 16.29); only 2% of days were ≥15°C. Lower air temperatures were often recorded at another sensor at BMR (Dendra, 2021), but rh was roughly equal for the two sensors.

At other places on the central California coast, we observed *T. occidentella* larvae developing upon naturally occurring scat and pellets. Where the scat or pellets sat upon on leaf litter, the floors of barns, or other hard substrates, the tubes stuck out from the food but did not enter the litter or wander over hard substrate. We have also reared *Tinea nivocapitella*, a closely related congener of *T. occidentella*, from scat and owl pellets at BMR and other places on the California coast. In contrast, none of the ca. 475 owl pellets collected beneath roost trees in Davis, CA over the course of this study produced *T. occidentella*. Davis CA is ca. 110 km inland with occasional high maximum humidity (≥ 80%) but hot (mean 29°C–34°C) summer weather (CIMIS, 2021).

Larvae in silk tubes but outside of pellets or scat became desiccated and died within several weeks in ambient laboratory conditions of ca. 45% rh to 55% rh, which indicated that the larvae need higher rh to survive. The data were inconsistent with diapause in this insect, generations of *T. occidentella* overlapped, and moths emerged from March – November, but did not emerge December – February in the field. However, they did emerge within a few weeks from pellets and scat brought into the laboratory, kept moist, and provided window light, in December. These emergences were as much as 2 months sooner than emergence began in the field. As well, pellets placed in a dark shed with field temperatures in November and kept moist, began pupating in early March and produced moths by late March, virtually identically mirroring times to maturity observed in the field. Rain in winter that wetted scat and pellets containing larvae did not result in early emergence in the field. These results indicated that very high relative humidity and temperature, but not day length or moisture from rain, contributed to development and maturation.

We did not observe *T. occidentella* moths, larvae, or pupae upon experimentally placed sheepskin or upon the fur of rabbit or deer cadavers in the field. We did not capture this species of moth in our funnel traps baited with undigested sheepskin, chicken manure, skatole, or traps left unbaited. We captured many moths of this species in the same traps containing owl pellets or coyote scat. In the lab, *T. occidentella* moths did not oviposit, nor did larvae feed, upon untreated sheepskin; three of ten larvae fed a small amount (but none pupated) upon the wool of sheepskin that had been soaked for 1 month in the dark liquid washed from scat and pellets. These results suggested that predator digestive treatment of fur was necessary to attract moths and for them to oviposit, feed, and grow. We observed no *T. occidentella* larvae or pupae in carnivore scat made up of fruit or crustacean parts that lacked fur or feathers.

T. occidentella moths laid eggs through an extruded ovipositor, and larvae developed upon scat and owl pellets as well as upon small experimental pellets made of fur from pellets (Figure 2a). Moths oviposited as readily into experimental pellets and whole owl pellets that we collected or purchased as into scat and pellets from the field.

Silk tubes

Larvae spun thick silk tubes and lived their entire immature lives within them (Figure 2b–f). Silk tubes spun by large larvae were ≈ 3 mm internal diameter (Figure 2b). The silk tubes absorbed moisture at high humidity. Tubes 20 mm in length, cleaned of sand and frass, had an average mass of 13.4 mg after drying in 40% rh for 12 h; the average mass of these tubes increased ≈ 15%, to 15.4 mg after 12 h at 99% rh. We infer from this that the larval tubes contribute to a high rh environment for larvae. The first few instars live in tubes inside the food (Figure 2c). Later instars spin extensions that range outward from the food. On the sandy substrate of BMR and on sand in the lab the tubes extended onto and into the substrate while remaining connected to the food through tubes that extend downward into the sand (Figure 2e). None of the thousands of tubes examined in the 7 years of this study passed near or ended in detritus, indicating the lack of evidence for alternative foods. Each subterranean tube was extended upward to the surface of the sand by the prepupae. Pupation occurred near the soil-air interface; the pupa (pharate adult) pushed the pupa partially out the tunnel end before eclosing and left the pupal shell that was extruded from the substrate (Figure 2f). In the sandy soil of the BMR some tubes penetrated to depths of 5 cm where the sand was moist and midday temperatures on clear summer days were much lower (≈10°C) than at the surface of the sand (≥40°C) (Figure 1e). During the day when the surface of the sand was hot, larvae were hidden in the refuges at bottom of the tubes that extended downward into the sand (Figure 1e). The larvae returned to the food source at night. When *T. occidentella* developed without sand, the silk tubes protruded outward from the pellet. While we have not been able to measure rh within the tubes because their diameter is less than our instruments, their silken tubes probably buffered larvae against low rh as well as high temperature. On hard substrates the pharate adult (pupa) pushed out of tubes extending from the food. We inferred that a primary role of the tubes was to provide a larval environment of high rh and mild temperatures.

Moisture, no food

Larvae of *T. occidentella* possessed a well-developed cryptonephric complex. Moreover, larvae showed no discontinuous spiracular ventilation, nor did they show bursting loss of CO_2 or water (personal communication, Jonathan Wright, see acknowledgements). Thus, we found no evidence that the larvae were highly permeable to water.

Scat and pellets dried to ambient conditions within 48 h of their production in nature, and they took up water from dew. The mass of water taken up overnight in an atmosphere of 99% rh by experimental, ≈200 mg fur pellets was ≈12% of the mass of pellets previously stored in ambient laboratory air of ≈45% rh.

In the laboratory, larvae outside of silk tubes lost mass at all values of rh when cultured without food. In 70% rh without food and outside of the silk tube, larvae lost between 2% and 12% of their mass after 24 h (Figure 3a). These results implied that *T. occidentella* cannot maintain water balance by means of water vapour absorption at 70% rh.

Subsequently, the larvae in Figure 3a were moved to 99% rh without food for 48 more hours, during which time they continued to lose mass (up to 30%) and began to die. Over the following 24 h at 99% rh with no food, most died and none of the 39 larvae in this experiment pupated. These results implied *T. occidentella* larvae cannot perform water vapour absorption at 99% rh. In addition, the result implied the importance of the silk tube for maintaining body water even at maximum relative humidity.

Larvae large enough to spin tubes outside of pellets were removed from their tubes and held at 45% rh without food for 48 h, at which time they showed no interest in a water drop placed next to them. In another experiment, a drop of water was placed on the anus of 12 larvae that had been held at 40% rh for 24 h; all attempted to move away from the droplet. Some cast a frass pellet immediately into the water as they moved away. All lost mass during the subsequent 24 h at 99% rh. 20 medium and large larvae were immersed individually in petri plates, each into 100 ml of water, and all died over night. Larvae in identical circumstances that were able to exit the water lived, but none gained mass. Thus, we found no evidence that instars large enough to construct a tube outside of the food source gain water by drinking or imbibing it through the anus.

Moisture and food

In preliminary work at 24.5 C in the lab, none of 23 first instars grown upon fur from owl pellets as food at ≤40% rh gained mass, and all died within a few weeks. At 99% rh, another 18 first instars all grew and 13 pupated between 44 and 74 days after hatching. With these observations in mind, we grew intermediate-sized larvae for 8 days upon experimental pellets of fur at: 77% rh, 88% rh, and 92% rh at 24.5°C (Figure 3b). The 33 larvae (11 in each rh replicate) had been cultured for 14 days in pellets at 99% rh. The larvae were weighed on day zero and day 8. All larvae fed and produced frass during the first few days, and all survived for the 8 days of this experiment. At 77% rh, only 6 of the 11 gained mass, and those not gaining ceased to produce frass by the end of the experiment. At 88% rh, 10 gained mass, and all produced frass throughout the experiment. At 92% rh all gained mass and produced abundant frass for the full 8 days. Larvae cultured at 88% rh increased in mean mass ca. two-fold over those grown at 77% rh. Those cultured at 92% rh increased in mean mass ca. 5-fold over those cultured at 77% rh and two-fold over those cultured at 88% rh (Figure 3b, Appendix A.2).

The combination of these results (lack of direct water vapour absorption by larvae, lack of measurable drinking by larger larvae, food absorbing water vapour, and growth rate increasing with increasingly high rh) suggests that the moisture source for *T. occidentella* is that absorbed in the fur and feathers that is their food, and the full capacity for growth is not realised at less than very high rh.

Geographic distribution of *Tinea occidentella*

Although the food sources of carnivore scat and raptor pellets are abundant throughout North America (see iNaturalist maps of owls and coyotes), the lion's share of records of *Tinea occidentella* are in the California coastal envelope that extends from Bodega Bay in the north into northern Baja California in the south (Figure 1, left, violet dots). This envelope has a mild maritime climate with very high rh, advective fog, and morning dew, and it lacks winter freezing and high summer temperatures. In contrast, the white dots in Figure 1 left show the iNaturalist records of 713 other species of moths, based upon 24,099 observations, by 3570 observers, (GBIF.org [28 July, 2021]) spread over the entirety of California. While locations of other moth species abundantly overlap the range of *T. occidentella*, the records for this species do not extend beyond the coastal envelope.

Considering the maximum daily rh during the growing season at the University of California Reserves within the coastal envelope, within 50 km of the coastline and within the area of reported *T. occidentella* observations, most had mornings between 95% rh and 100% rh, two reserves had most days close to 90% rh, and two more reserves had most days more than 80% (Dendra, 2021). None of these reserves recorded most days during the growing season with maximum rh less than 80%, nor did they record hard freezes or extremely hot temperatures or extended dry periods. Reserves further from the coast outside of the range of *T. occidentella* had low rh, extreme temperatures, or both (Dendra, 2021).

Multiple places farther inland in California had episodes of high rh in the growing season, but virtually none had the cool weather in the growing season where the insect is concentrated (CIMIS, 2021). The overwintering habitat of *T. occidentella* is within scat or pellets, which sit upon the ground exposed to the weather. Silk tubes that can extend down into substrates such as sand, where temperature extremes might be attenuated, could affect the distribution of this species.

DISCUSSION

Water balance

Water balance looms large in insects. For land dwelling arthropods in general, just as for terrestrial plants, gas exchange with the environment results in water loss (Mellanby & French, 1958); this is consistent with our results that showed non-feeding *T. occidentella* larvae lose mass even at very high rh (Figure 3a). For larvae of Coleoptera and Lepidoptera, the cryptonephric complex tubules of the hindgut provide adaptation to dry foods and dry environments via resorption of water from faeces (Kolosov & O'Donnell, 2019; Ramsay, 1976). As explained in Results, *T. occidentella* larvae possessed a cryptonephric complex and showed no tendency to be permeable to water. Some insects contribute to their moisture balance by drinking liquid water (Mellanby & French, 1958). The fog-basking tenebrionid beetles in the virtually rain-free environment of the Negev are a stunning example of insects that drink (Mitchell et al., 2020). However, our work found no evidence of drinking in *T. occidentella* by instars large enough to construct a tube outside of the food source. We were not able to assess drinking by the small instars that live inside the food. By oxidising food, some insects and especially those in dry environments can produce metabolic water (Chown & Nicolson, 2004); the domestic clothes moth *Tineola bisselliella* has been reported to produce metabolic water from its keratinaceous food (Chauvin, 1977). However, in the very moist developmental environment of *T. occidentella*, metabolic water would be so little as to be irrelevant.

Water vapour absorption is the fourth means by which some arthropods can obtain water. In this adaptation, atmospheric water vapour is condensed in fluids of high osmolality in the buccal or rectal cavity of arthropods (Machin, 1983). The threshold for uptake of water by this mechanism in a millipede has been observed at 85% rh (Wright & Westh, 2006). The single report of water vapour absorption by a lepidopteran was for the domestic pest *Tinea pellionella*, which was found in the laboratory to gain a tiny fraction of mass at 93% rh and above (Chauvin & Vannier, 1980). In our study, *T. occidentella* lost weight at 70% rh and 99% rh (without food), indicating no evidence for water vapour absorption by this insect (Figure 3a).

Our results indicate that *T. occidentella* obtain water from that absorbed from the atmosphere by the keratinaceous fur and feathers of their food. Hair absorbs water vapour at a greater than linear rate with increasing rh and can absorb up to ½ of its mass in water (Lévêque, 2004). Hydration via food is consistent with plant feeding, the dominant mode among Lepidoptera (Ramsay, 1976). Given this mode, obtaining water via the food could be seen as a pre-adaptation for keratophages, and should not seem surprising.

Records and distribution

Records of moth species derive from collections at lights, detections on food sources, and on substrates (Powell & Opler, 2009). *T. occidentella* is not collected or detected differently from other moth species, and it is distinctive and readily identified by the citizen scientists of iNaturalist (Figure 1, left, Appendix A.3). Records of all species of moths are spread broadly over the entire state of California, while *T. occidentella* records are concentrated along the coast of central and southern California (Figure 1, left).

The correlation between water absorption by food with the fog, dew and mild climate of its environment is a coherent explanation of the mesoscale restriction of *T. occidentella* to the coast. However, this explanation renders enigmatic the far-flung, scattered records of the species around western North America (Figure 1, upper right, Appendix A.3). While it is not unlikely that ground fog with dew occur during the growing season at these far-flung sites, all the area to the east of the coastal envelope has a continental climate with freezing in winter, high temperatures in summer, or both.

A tempting conjecture is that larval life with silk tubes extending into soil (Figure 2d–f) of riverbeds, lake shores, beneath logs, and other moist places that could afford escape from the temperature extremes beyond the coastal climate. Although we found no evidence for diapause in *T. occidentella* in California, the species could have diapause inland that would afford it a key adaptation to seasonal adversity (Bale & Hayward, 2010).

Another speculation derives from the fact is that while being very widely distributed, scat and raptor pellets are literally at the top of the trophic pyramid with biomasses that are orders of magnitude less than the vegetation food of plant feeding insects. This suggests population sizes of *T. occidentella* that are smaller than insects that feed upon litter or live plants; small population sizes would mean few dispersers and slow increase after colonisation of a new area. Sparse, far-flung populations could have lower probability of growth and persistence than populations within the coastal California envelope.

We see no temporal trend in temperature or relative humidity in the climate records at BMR (Shideler, 2021) or in the data of the other University of California reserves within the coastal envelope (Dendra, 2021). However, advective fog frequency on the California coast is decreasing (Roden et al., 2009). At the larger scale of the southwestern United States, the climate is warming and drying. The warming has caused more than three decades of loss of vegetation cover over the Sonoran Desert and mountains of Southern California (Hantson et al., 2021). A megadrought from 2000 to 2018 created the second driest pair of decades since 800 CE in southwestern North America, only the late-1500s was dryer (Williams et al., 2020). Insect declines are appearing with climate change (Wagner, 2020), and the megadrought has led to the loss of butterflies in the southwest (Wagner & Bailowitz, 2021). The questions of the effects of changing climate upon the distribution and abundance of *T. occidentella* will have to be addressed by further research.

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L. Wagner, Eric LoPresti, Mike Kaspari, and William Wetzel. The authors have no conflict of interest. The data are presented in the legends to Figure 3 and the Appendix A.

DATA AVAILABILITY STATEMENT

All data are in the appendix and figures of the manuscript.

ORCID

Donald R. Strong https://orcid.org/0000-0002-7227-5121
Christian John https://orcid.org/0000-0002-6249-040X

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

Promotional image 1. Tinea occidentella, lower right. Map (left) Locations of T. occidentella in California as violet dots. Locations of the 24,099 observations of 713 other moth species in California as grey dots. Map (upper right), T. occidentella range in the United States.

Promotional image 2. Tinea occidentella upon coyote scat. Note hair of the prey item in the scat, upon which the larvae of this moth feed.

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APPENDIX A

Data for Figure 3a

Larval mass of larval *Tinea occidentella* in mg at beginning of the experiment (abscissa, Figure 3a).

0.57, 1.67, 2.91, 2.95, 3.53, 5.1, 5.44, 6.61, 6.63, 8.84, 9.33, 9.81, 10.24, 10.6, 10.68,10.82. 10.96, 11.63, 11.7, 12.08, 12.3, 12.42, 13.34, 14.63, 14.83, 15.73, 15.79, 16.08, 16.29, 16.88, 18.24, 18.42, 19.6, 19.97, 20.88, 26.32

Larval mass of larval *Tinea occidentella* in mg after 24 h at 70% rh (ordinate, Figure 3a).

0.5, 1.47, 2.56, 2.67, 3.26, 4.7, 5.27, 6.11, 5.87, 8.48, 8.78, 9.08, 9.91, 10, 9.99, 9.97, 10.28, 11.45, 10.73, 11.34, 1, 1.49, 11.95, 12.6, 14.14, 14.22, 15.01, 14.78, 15.32, 15.2, 15.87, 17.31, 16.98, 18.3, 18.95, 19.74, 25.46.

Data for Figure 3b. Growth in mg of intermediate instar *Tinea occidentella* with food at relative humidity of 77%, 88%, and 92%. Each treatment had 11 larvae.

77% rh: 4.2, −4.9, −1.7, −1.2, 5.6, 3.4, 8.9, 2.88, −1.8, 4.3, −0.7.

88% rh: 8.9, 7.2, 5.1, 7.0, 10.1, 1.8, 5.5, 6.47, 6.51, 4.3, −0.1

92% rh: 5.1, 11.6, 9.4, 11.4. 14.3, 8.0, 5.5, 9.3, 13.0, 11.0, 13.9.

Museum and iNaturalist records of *Tinea occidentella* used in Figure 1, left and Figure 1, upper right

These records had recorded latitude and longitude.

Records were sourced through GBIF, the Global Biodiversity Information Facility. Categorization of points by state was accomplished using a state-level shapefile from the US Census Bureau; where points fell off the coast of California they were designated "California" (GBIF Occurrence Download [1 January, 2022] 10.15468/dl.4kf58n). The exception to GBIF sourcing were USNM personal communication (millers@si.edu) and CAS, California Academy of Sciences Insect Collection, https://monarch.calacademy.org/collections/listtabledisplay.php?db=allspec&taxa=Tinea+occidentella&usethes=1&taxontype=2). GBIF sourcing: ASUHIC, Arizona State University, Hasbrouk Insect Collection; iBOL, Biodiversity Institute of Ontario; CSU, Colorado State University, C. P. Gillette Museum; EMEC, Essig Museum of Entomology, California Insect Survey; iN, iNaturalist; INSDC, European Nucleotide Archive; LACNMHE, Los Angeles County Natural History Museum, Entomology; MCZ, Harvard University Museum of Comparative Zoology Entomology Collection; MISS, Mississippi Entomological Museum; SDNHM, San Diego Natural History Museum; USNM personal communication; YPM-ENT, Yale Peabody Museum, Entomology.

Source of Record	California	Arizona	Colorado	Texas	New Mexico	Nevada	Baja MX
ASUHIC	0	3	0	0	0	0	0
iBOL	7	0	0	0	0	0	0
CAS	43	0	0	0	0	0	0
CSU	3	0	0	0	0	0	0
EMEC	126	0	0	0	0	0	0
iN	86	0	4	1	0	0	2
INSDC	1	0	0	0	0	0	0
LACMNHE	7	0	0	0	0	0	0
MCZ	1	0	0	0	0	0	0
MISS	0	0	0	0	1	0	0
SDNHM	71	0	0	0	0	0	0
USNM-pers. comm.	0	11	0	2	1	1	0
YPM-ENT	1						