

# FLEA PARASITISM AND HOST SURVIVAL IN A PLAGUE-RELEVANT SYSTEM: THEORETICAL AND CONSERVATION IMPLICATIONS

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**ABSTRACT:** Plague is a bacterial zoonosis of mammalian hosts and flea vectors. The disease is capable of ravaging rodent populations and transforming ecosystems. Because plague mortality is likely to be predicted by flea parasitism, it is critical to understand vector dynamics. It has been hypothesized that paltry precipitation and reduced vegetative production predispose herbivorous rodents to malnourishment and flea parasitism, and flea parasitism varies directly with plague mortality. We evaluated these hypotheses on five colonies of Utah prairie dogs (UPDs; *Cynomys parvidens*), on the Awapa Plateau, Utah, US, in 2013–16. Ten flea species were identified among 3,257 fleas from UPDs. These 10 flea species parasitize prairie dogs, mice, rats, voles, ground squirrels, chipmunks, and marmots, all known hosts of plague. The abundance of fleas on individual UPDs (1,198 observations) varied inversely with UPD body condition; fleas were most abundant on lightweight, malnourished UPDs. Flea abundance on UPDs was highest in dry years that were preceded by wet years. Increased precipitation and soil moisture in the prior year might generate humid microclimates in UPD burrows (that could facilitate flea survival and reproduction) and paltry precipitation in the current year could predispose UPDs to malnourishment and flea parasitism. Annual re-encounter rates for UPDs (1,072 observations) were reduced in wetter years preceded by drier years; reduced precipitation and vegetative production might kill UPDs, and increased flea densities in drier years could provide conditions for plague transmission (and UPD mortality) when moisture returns. Re-encounter rates were reduced for UPDs carrying at least one flea compared to UPDs with no detected fleas. These results support the hypothesis that reduced precipitation in the current year predisposes UPDs to flea parasitism. Our results also suggest a link between flea parasitism and UPD mortality. Given documented connections between flea parasitism and plague transmission, our results point toward an effect of flea parasitism on plague-related deaths for individual UPDs, a phenomenon rarely investigated in nature.

**Key words:** *Cynomys*, disease ecology, *Oropsylla*, *Thrassis*, vector, *Yersinia pestis*.

## INTRODUCTION

Plague is a bacterial zoonosis of mammalian hosts and flea vectors. Field studies are needed to further scientific understanding of plague and to identify and refine mitigation strategies (D’Ortenzio et al. 2018). From the perspective of wildlife conservation, data are needed from areas where plague has been introduced (Biggins and Kosoy 2001; Gage and Kosoy 2006; Antolin et al. 2010). Plague is classified as an emerging infectious disease (Morens et al. 2004) and is among the zoonoses of top priority interest in North America (Centers for Disease Control and Prevention 2018).

In the grasslands of western North America, plague poses an enduring threat to prairie dogs (*Cynomys* spp.), colonial harem-polygynous sciurids. Plague fragments prairie dog

(PD) populations and depresses their densities (Cully and Williams 2001). In doing so, plague renders PDs incapable of serving their keystone functions (Antolin et al. 2002; Eads and Biggins 2015). Effective management of plague is critical at core conservation sites for PDs and species associated with them (Miller and Reading 2012).

Wildlife managers use information from studies of disease and vector ecology to strategize disease management (Russell et al. 2017). Considerable progress has been made on this front with PDs and plague (Abbott and Rocke 2012). Nonetheless, many studies require replication, and much remains to be learned (Richgels et al. 2016; Salkeld et al. 2016). In particular, it would be useful to further evaluate influences of flea parasitism

and weather on plague dynamics (Eisen and Gage 2012; Russell et al. 2018).

Considering flea parasitism, it seems probable that PDs harboring fleas are at greater risk of plague mortality than PDs carrying no fleas (although PDs can become infected when interacting with conspecifics, consuming infectious carcasses or fleas, manipulating infectious soils, etc.; Richgels et al. 2016). This flea hypothesis (Lorange et al. 2005), while supported by laboratory experiments with mice and rats (Eisen et al. 2009; Hinnebusch et al. 2017), requires evaluation with PDs and rodents in nature (Wilkening and Ray 2016).

Plague dynamics are also affected by the diversity of fleas and their preferences for hosts (Eisen et al. 2012). Flea species specializing on PDs play pivotal roles in transmitting plague bacteria to PDs (Wilder et al. 2008). Generalist fleas, with cosmopolitan tastes for hosts, can function as bridge vectors, facilitating the maintenance and spread of plague in mammal communities (Wimsatt and Biggins 2009; Eads et al. 2015). Prairie dogs live among a variety of rodents, and PDs carry specialist and generalist fleas, motivating research on flea-host relationships (Salkeld et al. 2016).

Precipitation and vegetative production also affect plague cycles (Eisen and Gage 2012). If precipitation and succulent vegetation are scarce, herbivorous PDs undergo reductions in body condition (Facka et al. 2010; Eads et al. 2016; Stephens et al. 2018). Malnourished rodents are immunocompromised and might reduce their grooming defenses against fleas (Krasnov 2008; Eads et al. 2016). Paltry precipitation might predispose PDs to flea parasitism (Eads et al. 2016), providing conditions for increased plague transmission in the current or subsequent year (Eads and Biggins 2017). If so, weather models might be used to strategize plague mitigation (Collinge et al. 2005; Savage et al. 2011; Russell et al. 2018).

We investigated flea and plague dynamics on colonies of Utah PDs (UPDs; *Cynomys parvidens*). Historically, UPDs occurred at high densities in Utah, US (Collier and Spillett 1973). Currently, UPDs are a federally

threatened species, existing mainly on fragmented colonies at three recovery units. It is well known that plague poses an imminent threat to UPDs (Hoogland et al. 2004). Nonetheless, relative to other *Cynomys*, few studies have investigated the ecology of fleas and plague on UPD colonies (Eads and Hoogland 2017; Rocke et al. 2017; Russell et al. 2018).

We studied the ecology of fleas and plague on five UPD colonies from 2013 through 2016. We evaluated 1) flea species diversity on UPDs; 2) factors affecting the abundance of fleas on UPDs, including precipitation and UPD condition; and 3) factors affecting UPD survival, including precipitation, UPD condition, and flea parasitism.

## MATERIALS AND METHODS

### Study species and sites

Field work was accomplished under the National Wildlife Health Center's Animal Care and Use Committee protocol number EP130214 (Rocke et al. 2017). We studied UPDs on the Awapa Plateau, Utah (38°11'N, 111°49'W). Vegetation includes shrub grassland with scattered stands of coniferous and aspen trees. The most common forage for UPDs includes blue grama (*Bouteloua gracilis*) and western wheat grass (*Pascopyrum smithii*; Lehmer et al. 2006). We live-trapped UPDs on five colonies from mid- to late-June through August 2013–16. We sampled greater than 90% of the areas occupied by UPDs on each colony based on mapped colony area. The collective area sampled at each colony ranged from 6 to 20 ha. The primary objective was to evaluate the effect of an orally delivered plague vaccine on UPD survival; vaccine effects were not detected at Awapa Plateau and, therefore, are not considered here (see Rocke et al. 2017).

Each year, each colony was trapped for a mean of 7 d (SD=2.34, range=4–11 d) on consecutive or nearly consecutive days, with sampling taking place from mid- to late-June through August. Elevations ranged from 2,645 m to 2,873 m. Each field season, we shifted from lower to higher elevations as the summer progressed. This approach helped to increase consistency in the amount of time between first emergence of adult UPDs from hibernation and our trapping efforts. In addition, we sampled each colony after juveniles had emerged from natal burrows, which occurs later at higher elevations.

### Animal capture and handling

Upon first capture each year, we anesthetized each UPD and fleas on its body (using isoflurane) and combed the UPD as thoroughly as possible over a white pan for 30 s to collect fleas (Biggins et al. 2010), which were stored in vials with saline (Russell et al. 2018). We recorded the age (juvenile or adult), sex, and mass (to the nearest 5 g) of each UPD and marked its ears with metal tags and body with passive integrated transponders, for permanent identification (Rocke et al. 2017). We indexed each UPD's body condition as the ratio between its weight and hind-foot length to the nearest 0.1 cm (weight:foot; Eads et al. 2016). Anesthetized UPDs were allowed to recover from anesthesia and released at their trapping locations.

### Flea identification and plague testing

Fleas were identified to species (Russell et al. 2018). Fleas from live-trapped UPDs, fleas from UPD carcasses found on or near the colonies, and UPD carcasses found in 2013–15 were tested for *Yersinia pestis* (Rocke et al. 2017). Plague was detected on one of the five UPD colonies in 2014 (a drought year preceded by wet conditions) and on three colonies in 2015 (an average year preceded by drought). Plague was not detected on any of the five UPD colonies in 2013 or 2016 (Rocke et al. 2017; Abbott et al. 2018; Russell et al. 2018). Prior research suggests that *Y. pestis* might have been circulating, at some level, among fleas and UPDs throughout our study, even in the absence of plague detection (Biggins et al. 2010).

### Environmental data

We were interested in the potential effect of forage production on flea parasitism and UPD survival. Although the Normalized Difference Vegetation Index is often used as a measure of vegetative production, its use is problematic when sites have complex vegetative structure (Pettoirelli et al. 2011), as was the case on four of the five UPD colonies. Thus, we concentrated on precipitation, which significantly influences abundance of blue grama, the most common UPD forage at all sites (Knapp et al. 2008).

To acquire separate estimates of precipitation for individual colonies each year, we used the Parameter-Elevation Relationships on Independent Slopes Model (Daly et al. 2008). The model uses a variety of information on weather and physiographic features to estimate precipitation at a resolution of 800 m (our study colonies were separated by a minimum of 1.6 km). We focused on precipitation from February through September, which encompasses the primary growing

season at Awapa Plateau and our sampling periods.

### Statistical analyses

We evaluated factors thought to correlate with the abundance of fleas on UPDs using negative binomial models, thereby accounting for a non-normal, skewed distribution of flea abundance (GLIMMIX, SAS® 9.3, SAS Institute Inc., Cary, North Carolina, USA). The models were run with a log-link function and maximum likelihood estimation. We started with a model containing the following predictor variables: precipitation of the prior year, precipitation of the current year, UPD age, UPD sex, and UPD condition. We also included an interaction between the two precipitation variables to evaluate how sequences of dry and wet years might affect flea parasitism; we consider this evaluation exploratory, because long-term data are better suited for such an assessment (Eads and Biggins 2017), but we were interested in trends from our 4-yr study. We reduced the model to a parsimonious form using Type III *F* tests and backward elimination ( $\alpha=0.050$  for main effects, 0.200 for the interaction).

To evaluate annual survival of UPDs, we used re-encounters of marked individuals as an index (White 1983). We ran a logistic regression model (GLIMMIX, SAS® 9.3, SAS Institute) with a log-link function. Each observation was a line of data for an individual UPD in a given annual interval; an animal must have been captured at the start of an interval to be included in that interval (e.g., a UPD captured in 2013 but not captured in 2014 was included in the interval 2013–14 but was not included in the interval 2014–15). The response variable was binomial (e.g., a UPD captured in 2013 and 2014 but not in 2015 received a response of 1 for the interval 2013–14 and a value of 0 for the interval 2014–15). Predictor variables included: precipitation of the prior year, precipitation of the current year, an exploratory interaction between the precipitation variables, UPD age, UPD sex, UPD condition, and flea parasitism of the prior year. We also included a control variable for trapping effort (i.e., trap days) in the current year. We converted flea abundance to a binomial variable of flea prevalence, i.e., the presence or absence of fleas on a UPD for the trapping session at the beginning of each re-encounter interval. A single infectious flea is sometimes capable of infecting a host (Eisen et al. 2009). Using our methods, there is a 94.6% probability that a trained technician will detect at least one flea on an anesthetized PD carrying at least one flea (Eads et al. 2013). We selected a parsimonious model using Type III  $\chi^2$  tests and backward elimination.

For all analyses, we present figures with predicted values of the response variable and 95% confidence intervals from model projections. We evaluated the goodness-of-fit for each interpreted model using a Pearson's  $\chi^2$  goodness-of-fit test statistic; values near 1.00 suggested good correspondence between observed and predicted values.

## RESULTS

Data are available from Eads et al. (2019a).

### Environmental data

Average historic cumulative precipitation from February through September of 1981–2017 was 288 mm at the lowest elevation colony and 355 mm at the highest elevation colony. Precipitation varied among colonies, but general trends were evident; on average, precipitation was 96% of the historic average in 2012, 129% in 2013, 78% in 2014, 106% in 2015, and 88% in 2016.

### Flea identification

We identified 3,257 fleas, 64% of which were *Thrassis francisi* and 20% of which were *Oropsylla tuberculata*. We also found *Oropsylla idahoensis* (8%) and *Oropsylla labis* (7%). *Thrassis francisi* was the most common flea, except at the highest elevation where *O. idahoensis* was most prevalent. *Oropsylla tuberculata* was found on all five UPD colonies. Additional flea species, each comprising less than 1% of all fleas, included *Aetheca wagneri*, *Catallagia* spp., *Eumolpianus eumolpi*, *Hoplopyllus anomalus*, *Rhadinopsylla sectilis goodi*, and *Thrassis stanfordi* (Supplementary Material Table S1).

### UPD flea parasitism

The assessment of flea abundance included 1,198 combings. Fleas were more abundant on adult than juvenile UPDs, on males than females, and on UPDs in poorer condition (Fig. 1 and Table 1). The exploratory interaction between the two precipitation variables demonstrated that flea abundance was high in dry years preceded by wet years (Table 1). The goodness-of-fit test statistic (1.44) dem-

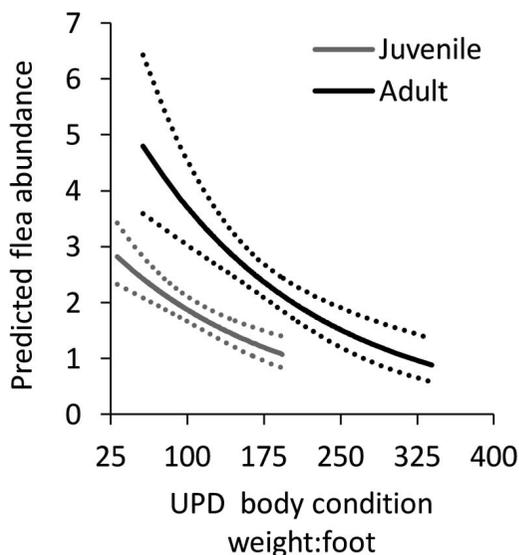


FIGURE 1. Multivariate model predicted flea abundance on individual Utah prairie dogs (UPD; *Cynomys parvidens*) on five colonies at the Awapa Plateau, Utah, USA, 2013–16, relative to UPD age and body condition; 95% confidence intervals are depicted as dotted lines.

onstrated good correspondence between observed and predicted values.

### UPD annual re-encounters

The initial assessment of UPD annual re-encounters included 1,054 observations. The variable for UPD condition was removed from the model ( $\chi^2_{1,1045}=1.99$ ,  $P=0.158$ ). The number of observations increased to 1,072 because body condition indices were missing for 18 observations. Re-encounter rates were higher for adult than juvenile UPDs, for females than males, and for UPDs that did not observably carry at least one flea in the prior year (Fig. 2 and Table 2). The exploratory interaction between the precipitation variables suggested UPDs were re-encountered least frequently in wet years preceded by low precipitation (Table 2 and Fig. 3). The goodness-of-fit test statistic (1.14) suggested good correspondence between observed and predicted values.

When considering the assessments of flea parasitism and UPD annual re-encounters in unison, UPDs were re-encountered most

TABLE 1. Type III  $F$  tests of fixed effects for the abundance of fleas on Utah prairie dogs (UPDs; *Cynomys parvidens*) at five colonies on the Awapa Plateau, Utah, USA, June through August 2013–16. Results are from a negative binomial generalized linear model.

Variable	Estimate	SE	$F$ value	$P$ value
Intercept	-6.371	3.983		
UPD age (adult)	0.673	0.124	29.55	<0.001
UPD sex (female)	-0.209	0.088	5.63	0.018
UPD condition	-0.007	0.001	29.59	<0.001
Prior precipitation	0.025	0.011	5.41	0.020
Current precipitation	0.015	0.010	1.96	0.162
Precipitation interaction	-0.0001	0.094	3.20	0.074

frequently under precipitation regimes that were associated with low flea parasitism (Fig. 3). Annual re-encounter rates were low if precipitation was scarce in the previous year and high in the current year (when fleas exhibited moderate abundance).

## DISCUSSION

We detected 10 flea species on UPDs that are collectively known to parasitize UPDs, mice, rats, voles, ground squirrels, chipmunks, and marmots. We might have underestimated flea species diversity, because we sampled fleas during short time periods each year on five UPD colonies. The three most prevalent

TABLE 2. Type III  $\chi^2$  tests of fixed effects on the annual re-encounter rates for Utah prairie dogs (UPDs; *Cynomys parvidens*) on five colonies at the Awapa Plateau, Utah, USA, June through August 2013–16. Results are from a binomial generalized linear model.

Variable	Estimate	SE	$\chi^2$ value	$P$ value
Intercept	31.571	10.817		
UPD age (adult)	0.595	0.207	8.26	0.004
UPD sex (female)	1.364	0.251	29.45	<0.001
Flea prevalence prior year (none)	0.716	0.210	11.58	0.001
Prior precipitation	-0.085	0.027	10.04	0.002
Current precipitation	-0.114	0.031	13.66	<0.001
Precipitation interaction	0.0003	0.0001	11.91	0.001
Trap days current year	0.249	0.053	22.23	<0.001

flea species (*Thrassis francisi*, *Oropsylla idahoensis*, and *O. tuberculata*) parasitize a multitude of rodents that host plague (Eisen et al. 2009), including species present at our field sites. For example, golden-mantled ground squirrels (*Callospermophilus lateralis*) and rock squirrels (*Otospermophilus variegatus*) inhabit the lower-elevation colonies; ground squirrels, chipmunks (*Neotamias* spp.), and marmots (*Marmota* spp.) occupy higher-elevation sites; and Great Basin pocket mice (*Perognathus parvus*), deer mice (*Peromyscus maniculatus*), canyon mice (*P. crinitus*), sagebrush voles (*Lemmyscus curtatus*), and chipmunks have also been documented at

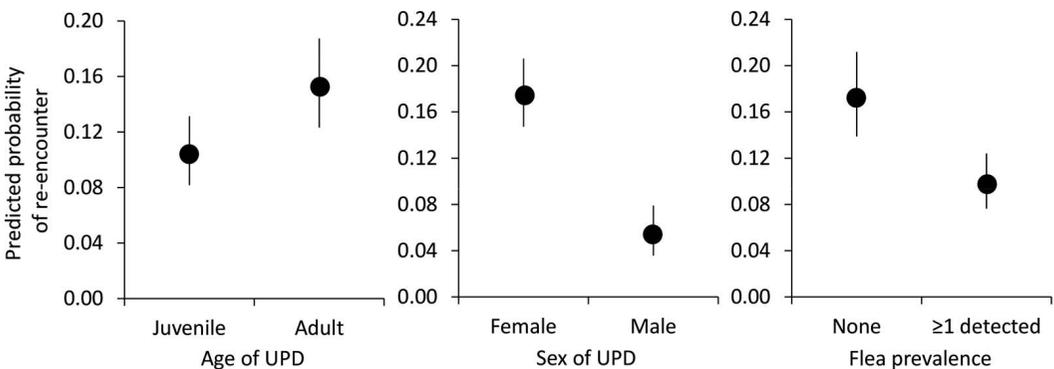


FIGURE 2. Multivariate model predicted probabilities of annual re-encounter (indices of annual survival) for Utah prairie dogs (UPD; *Cynomys parvidens*) on five colonies at the Awapa Plateau, Utah, USA, 2013–16, relative to age of UPD, sex of UPD, and the prevalence of fleas on UPD. Vertical error bars are 95% confidence intervals.

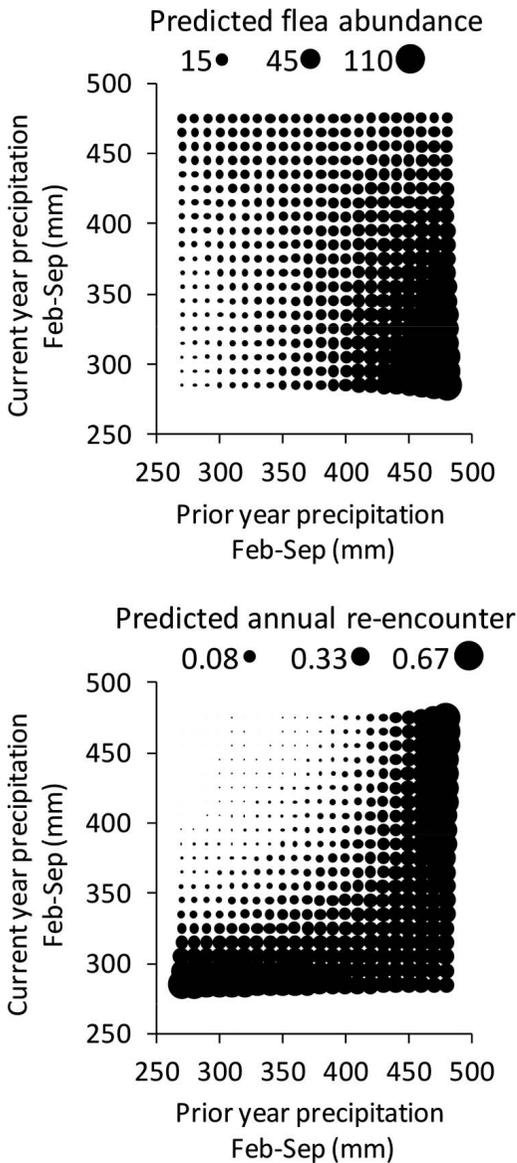


FIGURE 3. Multivariate model of predicted flea abundance per Utah prairie dog (UPD; *Cynomys parvidens*) and probabilities of annual re-encounter (indices of annual survival) for UPDs on five colonies at the Awapa Plateau, Utah, USA, 2013–16, relative to a statistical interaction between precipitation of the previous and current year. Predicted values increase with bubble size.

the study sites (Bron 2017). The large diversity of rodents and fleas at the Awapa Plateau might facilitate plague maintenance, given that the disease is a generalist of mammals (Biggins and Kosoy 2001). The

willingness of many flea species, with varying phenologies, to move among and parasitize many types of rodents is thought to facilitate plague maintenance and spread (Eisen et al. 2012; Ramakrishnan 2017) and might help to explain why plague is prevalent at high elevations in Utah (Arjo et al. 2003). Cool mesic conditions throughout much of the Awapa Plateau might be beneficial for ectothermic fleas that are prone to desiccation under dry conditions (Krasnov 2008) and beneficial for *Y. pestis*, which seems to be transmitted more efficiently by fleas at lower temperatures above freezing (Williams et al. 2013).

We detected a negative correlation between flea prevalence and UPD survival, supporting the hypothesis (Lorange et al. 2005) that flea parasitism on individual rodents positively correlates with plague transmission and mortality. This result is persuasive because we compared data from flea-parasitized and flea-free UPDs living under similar ecological conditions on the same colonies. However, we could not determine how many of the UPDs carrying fleas were killed by plague or disappeared for other reasons, and the assessment of precipitation regimes was correlative and included a small number of years. Flea abundance varied inversely with UPD body condition. The UPDs harboring fleas might have died from plague or because they were in poor condition. Although it is also possible that flea parasitism itself lead directly to mortality, such effects have only been documented during field studies in which lethal diseases were not accounted for or lab studies (Hawlena et al. 2006; Devevey and Christe 2009; Patterson et al. 2013).

Fleas were most abundant when precipitation was plentiful in the previous year and scarce in the current year. When precipitation is plentiful, relatively large amounts of water can percolate underground. However, it could take several months or more for the moisture to reach UPD nests (Ben Ari et al. 2011), which are often more than 1 m underground (Verdolin et al. 2008). Once the moisture

arrives at a UPD nest, it could moisten soils there (Eads 2014) and, in doing so, create a humid microclimate that (if not too sodden) benefits desiccation-prone fleas (Krasnov 2008). Reduced precipitation in the current year and consequent reductions in vegetative production can predispose rodents to poor body condition, weakened ectoparasite defenses, and increased flea parasitism. Consequently, the abundance of fleas on individual hosts can increase in dry years (Eads et al. 2016; Eads and Hoogland 2016, 2017).

The UPD annual re-encounter rates were low when precipitation was scarce in the previous year and high in the current year, that is, when fleas exhibited moderate abundance. In the context of plague mortality, it is possible that moderate flea densities are sufficient to spark feedback cycles that increase plague transmission and reduce UPD survival. Flea-host ratios can increase rapidly, even from a moderate starting point (Biggins and Eads 2019). Following an initial UPD focal infection and mortality event (Gage 2012), moderate numbers of fleas on the dead UPD can seek and find a live UPD, increasing its flea load (Tripp et al. 2009) and producing a secondary focal infection and mortality event; this feedback cycle can continue as plague infections, flea parasitism, and UPD mortality increase.

Many years of data are required to test for lagged effects of environmental variables on ecological dynamics, because each year of data at each site represents an  $n=1$ . In the context of plague, this issue is further compounded by the fact that this disease is predicted by a complex suite of ecological interactions (Barnes 1982, 1993). Although we present data from only 4 consecutive yr, we did survey UPDs at five separate sites. Our assessment of UPD re-encounters, a potential proxy for plague effects, provides support for the hypothesis (Lorange et al. 2005) that flea parasitism varies directly with plague mortality and adds to accumulating evidence supporting the hypothesis (Eads and Biggins 2017) that sequences of dry-to-wet years facilitate plague transmission.

Much research on UPDs has concentrated on forage, because low forage production reduces UPD condition and reproduction (Cheng and Ritchie 2006; Elmore and Messmer 2006). Our results on UPD condition (Fig. 1) suggest low forage production could increase the susceptibility of UPDs to flea parasitism and, perhaps, plague transmission (e.g., when moisture returns). Habitat quality and plague might have interactive effects on UPDs, for instance due to the effects of forage on UPD water balance and condition, and effects of precipitation and forage production on flea parasitism, host densities, and plague transmission (Eads et al. 2016; Eads and Hoogland 2016, 2017; Eads and Biggins 2017). Put differently, the effects of habitat and plague on UPDs are potentially confounded (Hefley et al. 2017). In the future it would be valuable to use an experimental approach to evaluate the individual, collective, and interactive effects of habitat quality and plague prevalence on UPD populations, for example, by using prescribed burns or irrigation to manipulate habitat, and pulicides to manipulate fleas and plague.

In summary, we found a large diversity of flea species on UPDs at the Awapa Plateau. We detected a link between flea parasitism and UPD survival, perhaps due to plague. The correlative link between flea parasitism and UPD survival encourages the use of flea control measures for plague management on UPD colonies (Biggins et al. 2010; Matchett et al. 2010; Eads and Biggins 2019; Eads et al. 2019b).

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### SUPPLEMENTARY MATERIAL

Supplementary material for this article is online at <http://dx.doi.org/10.7589/2019-08-201>.

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