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The invasive acanthocephalan parasite *Pachysentis canicola* is associated with a declining endemic island fox population on San Miguel Island

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ABSTRACT

In the late 1990s, the San Miguel Island fox (*Urocyon littoralis littoralis*) faced near-extinction. Fourteen of the 15 remaining foxes were placed into an island-based captive breeding program used to repopulate the island. Although the fox population in San Miguel reached pre-decline numbers by 2010, a second decline started around 2014, coincidental with a newly observed acanthocephalan parasite. To identify this introduced acanthocephalan species and determine the pathologic consequences of its infection on the health of foxes, we used an extensive record of island fox necropsies and associated parasite collections. In addition, we used detailed fox capture-recapture data to investigate population health and demographic trends of foxes before and after parasite emergence. We identify the parasite as *Pachysentis canicola*, a common acanthocephalan in mainland foxes in North America. The parasite was detected in 69% of the necropsied foxes from San Miguel Island and was not found in any of the other five Channel Island fox subspecies. Health impacts attributed to the acanthocephalan parasite, including erosive and ulcerative enteritis, transmural necrosis, and inflammation, were described in 47% of the foxes infected with the acanthocephalan. Despite infection with various other helminth parasite species, body condition remained good and the mortality rate low in San Miguel Island foxes until the arrival of the acanthocephalan. Body condition improved after 2018, perhaps due to increases in rainfall following a drought, but remained 27% lower than the pre-acanthocephalan period, which suggests that environmental conditions and parasitism jointly drive fox population dynamics.

1. Introduction

The Channel Island fox (*Urocyon littoralis*) lives on six of the eight California Channel Islands (Wayne et al., 1991). These islands range in size from Santa Cruz, the largest island at 250 km^2, to San Miguel, the smallest fox island at 38 km^2 (Rubin et al., 2007). The San Miguel Island fox (*Urocyon littoralis littoralis*) (hereafter referred to as SMIF) is an endemic subspecies found exclusively on San Miguel Island. It is the island's top predator and an object of considerable public adoration, as evidenced by a well-organized non-profit organisation called “Friends of the Island Fox” (www.islandfox.org). In 1987, the California Department of Fish and Wildlife, USA, designated several island fox subspecies as threatened, and by the late 1990s, fox subspecies in the northern islands faced near-extinction due to hyper-predation by golden eagles, initially attracted to the islands by the presence of

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introduced pigs and deer (Roemer et al., 2001, Roemer et al., 2002). In 1999, the Channel Islands National Park launched on-island captive breeding and habitat restoration strategies, encompassing the removal of non-native pigs and deer, as well as the translocation of golden eagles to the mainland (Coonan, 2003). On San Miguel, 14 of the 15 remaining SMIFs were captured for protection from predation and participation in an on-island captive breeding program (Coonan and Rutz, 2001). Captive-bred SMIFs were released starting in 2004, culminating in a rapid recovery of the population, which reached pre-decline numbers by 2010 (Coonan, T.J., Schwemm, C.A. 2009. Factors contributing to success of island fox reintroductions on San Miguel and Santa Rosa Islands. In: Damiani, C.C., and Garcelon, D.K., (Ed.), Proceedings of the 7th California Islands Symposium. Institute for Wildlife Studies, Arcata, CA, USA, pp. 363–376). Because endangered canids have extremely low reintroduction success rates (Ginsberg, 1994; Boitani et al., 2004), the Island Fox Recovery Program became an example of a well-planned and executed conservation action. Although the island fox populations on other northern Channel Islands continued to thrive, the SMIF population declined noticeably between 2014 and 2018 to 30% of its population peak (Dillon and Shaskey, 2022). This decline was coincidental with the discovery in 2012 of an unidentified acanthocephalan parasite, not found on any other of the Channel Islands and never before reported in island foxes. Concurrently, an increased proportion of trapped SMIF were in poor body condition and higher mortality rates were hypothesized to be due to severe acanthocephalan infections (Dillon and Shaskey, 2022).

Acanthocephalans (thorny-headed worms) are intestinal parasites of vertebrates (Taylor et al., 2007). Although they rarely infect humans or cause significant disease in domestic animals, in particular circumstances infections are fatal and can cause host population decline (Kennedy, 2006). The adult female worm lays eggs that are passed into the environment via the host feces, where aquatic or terrestrial arthropods ingest them, becoming intermediate hosts. The cycle is completed when a definitive host ingests the arthropod, and the cystacanth develops into a new adult worm (Kennedy, 2006; Taylor et al., 2007; Saari et al., 2019). Acanthocephalan species that infect foxes in the Americas include *Pachysentis canicola*, known to infect the island foxes' ancestor, the gray fox (*Urocyon cinereoargenteus*) (Buechner, 1944). Additionally, *P. canicola* infects coyote (*Canis latrans*) (Drewek, J. 1980. Behavior, population structure, parasitism, and other aspects of coyote ecology in Southern Arizona (Doctoral dissertation). The University of Arizona, Ann Arbor, Arizona, United States) and various skunk species such as *Conepatus leuconotus*, *Mephitis mephitis*, and *Spilogale gracilis* (Neiswenter et al., 2006), among several other mammals in North America (Amin et al., 2022). Another noteworthy acanthocephalan species is *Prosthenorchis cerdocyonis* (Gomes et al., 2015), which parasitizes the crab-eating fox (*Cerdocyon thous*) in the Brazilian Pantanal wetlands (Gomes et al., 2015), and sometimes emerges as a problem in zoo animals (Zárate-Ramos et al., 2018). The parasite diversity of island foxes has been monitored for many years by various conservation programs, using methods such as coprological analyses for detecting parasites and detailed necropsies of deceased foxes (Coonan and Rutz, 2001; Coonan and Rutz, 2002). Remarkably, an acanthocephalan parasite was never reported on any of the Channel Islands until 2012, when it was discovered on San Miguel Island.

The pathogenicity of acanthocephalans depends on the intensity of infection and the extent the proboscis penetrates into the host tissue (Kennedy, 2006). Acanthocephalan species with short necks typically penetrate little. Conversely, species with elongated necks, such as *Pachysentis canicola,* can penetrate into the intestine wall, causing the formation of fibrous nodules visible from the exterior intestinal surface (Taraschewski, 2000). In addition, the hooks in the parasite's proboscis cause a strong inflammatory response, leading to necrosis and, ultimately, intestinal perforation. Further, heavy infections can result in intestinal obstruction and invasion/migration of the parasite into the abdominal cavity (Kennedy, 2006). Such infections can be fatal. There is virtually no information on the sublethal effect of acanthocephalan parasites in wildlife. However, acanthocephalan infection causes degeneration and loss of the intestinal villi, and the formation of granular and fibrotic tissues associated with host immune responses, leading to decreased intestinal digestive and absorptive efficiency (e.g., Sanil et al., 2011). This and other mechanisms are hypothesized to cause sublethal effects in the acanthocephalan hosts (Taraschewski, 2000; Kennedy, 2006).

The objectives of our research were to: (i) identify the acanthocephalan parasite to species, (ii) identify its intermediate host, (iii) tabulate the consequences of the acanthocephalan parasite on the health of individual foxes via necropsy, (iv) measure changes in trends of fox population health before and after acanthocephalan discovery, and (v) statistically test hypotheses about the parasite's role in the decline of the SMIF population.

2. Materials and methods

2.1. Individual fox health

We summarized information obtained from necropsies of SMIFs performed between 2005 and 2022. All necropsies from 2005 to 2010 were performed in the laboratory of Linda Munson in the School of Veterinary Medicine at the University of California Davis, USA. Necropsies performed from 2010 to 2022 were performed at the California Animal Health and Food Safety Laboratory, School of Veterinary Medicine, USA, by one pathologist certified by the American College of Veterinary Pathologists (coauthor L. Woods). Necropsied foxes were sourced from two primary channels: mortality events detected during routine monitoring of the over 50 collared foxes maintained by the National Park Services on the island and incidental mortality events discovered by biologists and researchers during regular field activities. Every fox carcass was evaluated using a Channel Island fox protocol to ensure each necropsy was consistent and thorough. Body condition and postmortem condition were evaluated, and each organ system was thoroughly evaluated including intestines, which were completely opened. Parasites were identified visually. All organ systems were examined microscopically to evaluate histopathological changes. We calculated the probability of false negative detections before 2012 for San Miguel and during the entire study period for other Channel Islands (Santa Rosa, Santa Cruz, San Nicolás, Santa Catalina, and San Clemente), (a simple formula for the probability of not observing an infection in a sample of hosts where a parasite is present is $(1\text{-}p)^n$ where p is prevalence and n is sample effort, assuming random sampling and perfect detection in an infected animal).

2.2. Parasite investigation

2.2.1. Identifying the acanthocephalan

Identification was done by morphological and molecular methods, with a focus on distinguishing between *Pachysentis* and *Prosthenorchis*. Acanthocephalan parasites collected from the small intestines of necropsied SMIFs were prepared for microscopic examination (Richardson, 2006) as modified by Richardson and Barger (2006). Before DNA extraction, a tissue fragment was cut (hologenophore, Pleijel et al. (2008)), and molecular analyses were conducted according to Richardson et al. (2010). DNA was isolated from four individual specimens (mifM287 #2, 28A M278, 1080 F400 and 6B 101F317) as well as from one whole specimen (25A F370) with the DNeasy Blood & Tissue Kit from Qiagen, Inc. (USA) (cat. no. 69504), following the protocol for animal tissues given for the purification of total DNA using spin-columns. For the proteinase K treatment step, tissue samples were lysed overnight at 56 °C. DNA was eluted from the spin columns with 150 μl of AE buffer from Qiagen Inc.

PCRs were prepared using the Illustra PuRe Taq Ready-To-Go PCR beads from GE Health Care (USA) (cat. no. 27-9559-01). Primers were purchased from Integrated DNA Technologies (USA) and comprised two primers each for cytochrome c oxidase subunit I (COI) as specified by (Folmer et al., 1994) and (Light and Siddall, 1999). Specifically, the COI primers were LCO1490 (5′-GGTCAA CAAATCATAAAGATATTGG-3′) and HCO2198 (5′-TAAACTTCAGGGT GACCAAAAAATCA-3′). Primers for 28S were LE28SBo (CCCA-CAGCGCCAGTTCTGCTTACC) (Prendini et al., 2005) and LE28SA (GACCCGTCTTGAAGCACG) (Whiting, 2002). Primers for the 18S gene were 18SU467F (5′-ATCCAAGGAAGGCAGCAGGC-3′) and 18SL1310R (5′-CTCCACCAACTAAGAACGGC-3′) (Suzuki et al., 2008) and BD1 (5′-GTCGTAACAAGGTTTCCG TA-3′) and BD2 (5′-TATGCTTAAATTCAGCGGGT-3′) (Galazzo et al., 2002) for ITS1 + 5.8S + ITS2 region.

The final volume of PCRs was 25 μl and DNA was amplified under the following PCR conditions: 94 °C for 5 min; 35 cycles of (94 °C for 30 s, 50 °C for 30 s, 72 °C for 45 s); 72 °C for 8 min. Following PCR, samples were cleaned up using a QIAquick PCR purification kit from Qiagen (cat. no. 28104). Purified PCR products were sequenced using the above primers by the W.M. Keck Foundation Biotechnology Resource Laboratory at Yale University, USA. DNA sequences obtained during the study for COI, 28S, 18S, and ITS1 + 5.8S + ITS2 genetic regions of *P. canicola* were manually edited and a BLASTn search (https://blast.ncbi.nlm.nih.gov/https://blast.ncbi.nlm.nih.gov/) was used to search for similarities with sequences from GenBank®.

2.2.2. Identifying the intermediate host

Invertebrates were collected on San Miguel Island between November 2018 and March 2021, with a particular focus on arthropods hypothesized to be intermediate hosts for acanthocephalan parasites and other SMIF parasites. Invertebrates were collected by opportunistic hand capture, inspection under boards set up for herppetofauna monitoring, transects baited with oatmeal, cups placed on trails in shallow, existing holes, and hand collection on and around fox scat (for more details see Childress, J.N. 2023. The Parasite Ecology of the San Miguel Island Fox, *Urocyon littoralis littoralis* (Doctoral dissertation). University of California, Santa Barbara, California, USA). Insects (e.g., beetles, crickets) and gastropods (e.g., snails) are common intermediate hosts for acanthocephalan parasites, so they were the primary targets of our survey. Pitfall and other common invertebrate collection traps were not used so as to preserve Native American Chumash heritage sites and to reduce the potential of encountering unexploded ordnance (San Miguel Island is a former explosive test site of the US military) (William et al., 2017). After collection, invertebrates were identified by morphology from a selection of known species from San Miguel Island. Hosts were dissected fresh on-site or after freezing. The dissections were targeted to find intermediate stages of acanthocephalan parasites with particular attention to its infective stage, the cystacanth, which is relatively large, distinct, and found in the hosts' body cavity. The cystacanth has all of the structures of the adult parasite and only differs in its smaller size and the degree of sexual development (Schmidt and Nickol, 1985).

2.3. Fox population effects

The SMIFs were monitored by Channel Islands National Park field biologists using mark-recapture trapping methods to estimate the annual population size. The trapping scheme consisted of four large 18-trap grids (6 × 3) with traps separated by ~250 m. Trapping grids were run each September since 2008 for five consecutive nights (checking traps daily). Additionally, transect trapping across the island was performed on a regular basis between July and January to implement different management actions, significantly increasing the trapping effort each year. Captured foxes were marked with a unique passive integrative transponder (PIT) tag, aged into a pup or non-pup group, and assigned to one of five categories of body condition based on external appearance: (1) emaciated, (2) thin, (3) optimal, (4) overweight, and (5) obese. Additionally, all foxes were weighed when captured using a Pesola digital hanging scale (Switzerland). The trap was first weighed with the fox inside and then weighed separately after the fox was released. Trap weight was subtracted from fox-in-trap weight to calculate the fox's weight. In total, data from 4269 captures of 846 separate foxes were used in the analyses.

First, we summarized the information on body condition and weight of SMIFs between 2006 and 2022, using captures from the main trapping protocol run in September. We used several different analytical approaches to determine if the distribution of fox body condition and weight in the population changed after the acanthocephalan parasite was detected on the island. To determine differences in the odds of having a low body condition among years, we conducted a cumulative link (mixed) model analysis, also known as ordinal regression models (Armstrong and Sloan, 1989), that accounts for the order of the categories in the dependent variable. We used individual body condition as the dependent variable, year of capture as a categorical independent variable using 2011 (the last year before the acanthocephalan was detected on the island) as a reference level, and fox ID as a random effect. When the same fox was captured more than once per year, we used the most common body condition recorded (i.e., mode). We used binomial generalized linear mixed models (GLMM; logit link) to investigate the interaction between precipitation during the previous rainy season and the arrival of the acanthocephalan parasite on the island, and their association with body condition. Precipitation data for San Miguel was sourced from the Daily Surface Weather and Climatological Summaries (DAYMET) website (https://daymet.ornl.gov/). The daily precipitation in San Miguel during the study period was sampled at 10 random points on the island and then averaged monthly. The binomial response variable was two body condition categories (LowBC = categories 1 and 2, HighBC = categories 3 and 4, no foxes in body condition 5 were registered during the study period), and fox ID was included as a random effect. Several models with the combination of the fixed effects of precipitation, the presence/absence of the parasite on the island, and their interaction were compared using the Akaike Information Criterion (AIC). When the ΔAIC between the best candidate models was less than 2, we considered model simplicity or parsimony for final model selection, under the assumption that adding new variables did not significantly improve model performance. The same analyses were conducted using fox weight as the dependent variable and a Gaussian instead of a binomial distribution. In addition, we conducted an intervention analysis using the first parasite identification in 2012 as the intervention date. Intervention analysis (Box and Tiao, 1975) allows one to determine if the mean level of a time series changes after an intervention event, assuming a similar time series structure before and after the intervention. We used the yearly proportion of high body condition (i.e., conditions scores 3 and 4) in SMIFs as the time series indicator variable and precipitation during the previous rainy season as a covariate. These analyses were performed using the packages glmmTMB (Brooks et al., 2017), Ordinal (Christensen, R. H.B. 2023. ordinal—Regression Models for Ordinal Data. R package version 2023.12-4.1. https://CRAN.R-project.org/package=ordinal) and CausalImpact (Brodersen et al., 2014) in R.

Because environmental conditions, particularly rainfall, are relevant to population dynamics of island foxes in other Channel Islands (Bakker et al., 2021), we considered how survival was associated with body condition and precipitation using a Bayesian multi-state Cormack-Joly-Seber (CSJ) capture-recapture model (Royle and Dorazio, 2012) with data augmentation, temporal random effects, and three demographic states: pups, adults in low body condition (conditions scores 1 and 2), and adults in high body condition (conditions scores 3 and 4). In addition, to control for seasonal differences in capture efforts and fox traits (e.g., body condition), we included three seasons in the analysis: Season 1 = July and August, Season 2 = September to November, and Season 3 = December and January. We used uninformed uniform priors between 0 and 1 for all state-specific survival and transition probabilities throughout the model and assessed model convergence through visual assessment of trace plots, using Gelman and Rubin's diagnostic statistic (R-hat < 1.2) (Gelman and Rubin, 1992). We sampled from the posterior distributions using Markov-Chain Monte Carlo (MCMC) with three chains of 25,000 iterations. We discarded the first 5,000 iterations of each chain as burn-in. Model fitting was done using NIMBLE (de Valpine et al., 2017).

2.4. Data accessibility

A data release for this paper is not currently available due to the diversity of contributors, some of which have ongoing data collection efforts. However, readers interested in a particular data set used here may contact OAA or the author responsible for curation and dissemination: genetics (DR), necropsies (LWW), mark-recapture (JTS and SB), invertebrate dissections (JNC), code and analyses (OAA).

3. Results

3.1. Individual fox health

Necropsies were performed on 499 foxes from San Miguel (*n* = 55), Santa Rosa (*n* = 31), Santa Cruz (*n* = 30), San Nicolás (*n* = 75), Santa Catalina (*n* = 154), and San Clemente (*n* = 154) Islands between 2010 and 2022. Acanthocephalans were found exclusively on San Miguel Island, in 36 SMIF carcasses with intact intestines (intestines had been scavenged in two carcasses). Even with a limited number of necropsies (*n* = 16) before 2012 on San Miguel (Supplementary Fig. S1), the probability that the sampling program failed to observe an acanthocephalan was less than one in 300 million with the currently observed prevalence, and less than 0.5 for prevalences as low as one in 23 foxes (17 times lower than the post-2012 prevalence of 0.66). Similarly, between 2010 and 2022, the probability of failing to detect an acanthocephalan infection was less than 0.5 for prevalences as low as one in 108 in San Nicolas, one in 43 in Santa Cruz, one in 44 in Santa Rosa, and one in 222 in both San Clemente and Santa Catalina. Thus, although it is impossible to say that the acanthocephalan never occurred outside San Miguel Island or before 2012, our methods were highly likely to have detected even relatively low prevalence infections.

Acanthocephalans were firmly attached to the mucosa, and the highest mean intensities of adult worms were observed in 2014 and 2015, with 30 (range 1–103) and 22 (range 2–72) adult worms per infected fox, respectively. Acanthocephalans were 6–14 mm long and 2–4 mm wide. Most had transverse folds (accordion-like), which could be pulled apart to full length. Eleven (30%) of the foxes infected with *P. canicola* had peritonitis associated with the infection (Fig. 1A and B). At the initial inspection, foxes positive for the acanthocephalan parasite were in poor body condition and emaciated. Foxes with peritonitis had frothy, creamy, red-tinged exudative effusion in the peritoneal cavity overlying multifocal (Fig. 1B) or diffuse (Fig. 1A), thickened, dull, fibrinous serosa. Peritonitis was the definitive cause of death in these foxes.

Parasite intensity correlated with pathology. The small intestines of foxes with acanthocephalans were dilated and flaccid. The walls of the small intestines were diffusely thickened, and the mucosa had a granular appearance. The serosal surface of foxes without peritonitis was slightly dull, and there were multifocal 2–4 mm black pigmented foci.

Microscopically, the intestinal mucosa of less severely affected foxes had multifocal, superficial to mid-mucosal necrosis and multifocal, widely scattered crypts that were distended with mucus and lined by attenuated epithelium (Fig. 2A). Other crypts were hyperplastic and tortuous. Acanthocephalans were embedded to various depths in the mucosa; some penetrated through the mucosa and into the submucosa and muscularis. Necrosis, pleocellular inflammation (including neutrophils, macrophages, and lymphocytes), and fibrosis were observed at the leading edge of the proboscis of the acanthocephalans, and bacteria were abundant in the space between the parasite and host intestine (Fig. 2B). Penetration of the parasite and associated inflammation and necrosis were transmural in foxes with peritonitis. The intralesional parasite had a pseudocoelom, an anterior proboscis with hook-like projections, and no digestive tract. There was a thin peripheral cuticle, thick hypodermis composed of a subcuticular felted layer, and a thickened inner layer of cross fibers occasionally interrupted by lacunar channels and two layers of muscle (circular and longitudinal bordering the pseudocoelom).

3.2. Parasite investigation

3.2.1. Identifying the acanthocephalan

The five specimens examined in this study (mifM287 #2, 28A M278, 1080 F400, 6B 101F317, 25A F370) were morphologically consistent with *P. canicola* (Fig. 3), as described by Van Cleave (1953) and expanded by Amin et al. (2022). Identification was confirmed by molecular analysis utilizing the ITS1 + 5.8S + ITS2 DNA sequences (GenBank accession numbers **PQ186359-PQ186363**). The specimens examined were 95 to 96% identical to specimens submitted by Amin et al. (2022), with 25 differences in 640 nucleotides and nine gaps. Due to the paucity of molecular data present in GenBank for *P. canicola,* sequences for 28S (**PQ192565-PQ192569**) and 18S (**PQ187850-PQ187854**) were also deposited.

3.2.2. Identifying the intermediate host

A total of 945 invertebrates from at least 21 different genera were dissected, but no cystacanths were found. The specimens dissected included the orders Coleoptera, Dermaptera, Gastropoda, Hemiptera, Hymenoptera, Isopoda, Orthoptera, and Zygentoma. The dissections were conducted across all four seasons, with most occurring during late winter/early spring (*n* = 522) and autumn (*n* = 329) (Supplementary Table S1).

3.3. Fox population effects

The body condition and weight of foxes decreased after *P. canicola* was first detected on San Miguel Island (Fig. 4, Supplementary Fig. S2). Before the acanthocephalan was detected in

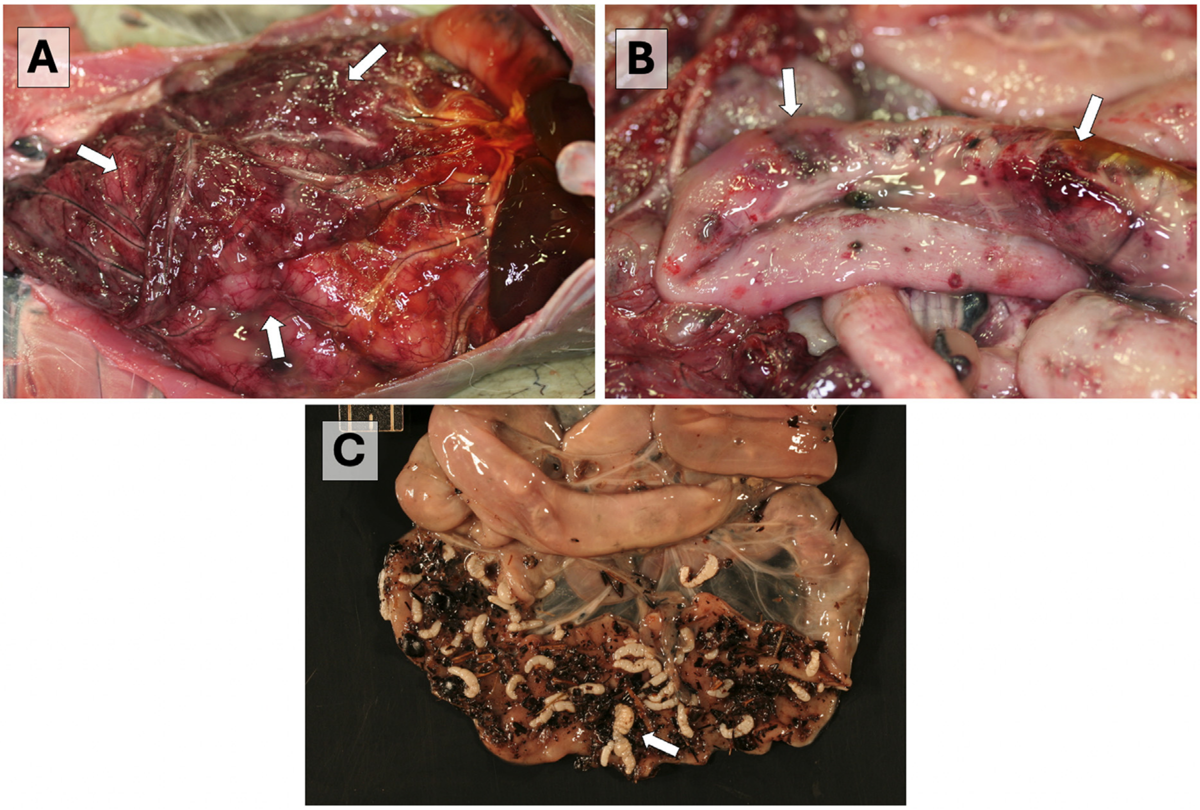

Fig. 1. The digestive tract of San Miguel Island fox (*Urocyon littoralis littoralis*) with the acanthocephalan parasite, *Pachysentis canicola*. (A) Diffuse peritonitis with thickened, hemorrhagic mesentery overlaying the gastrointestinal tract (arrows). (B) Multifocal peritonitis associated with transmural necrosis (arrows) in the small intestines caused by *P. canicola*. (C) Opened loop of flaccid, dilated small intestines with large numbers of adherent *P. canicola* (arrow).

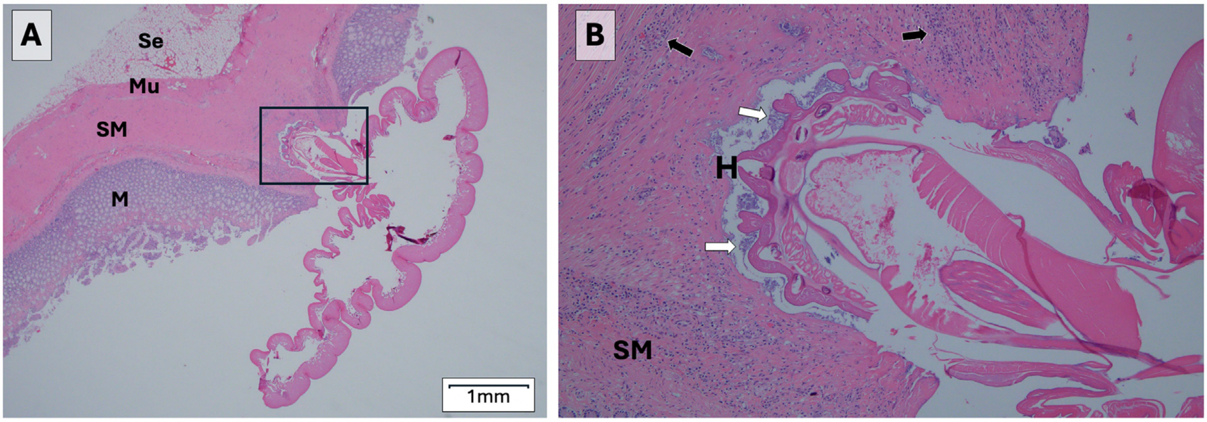

Fig. 2. Full-thickness section of the intestine (M, mucosa; SM, submucosa; Mu, muscularis and Se, serosa) of a San Miguel Island fox (*Urocyon littoralis littoralis*) infected with the acanthocephalan parasite *Pachysentis canicola*. (A) *Pachysentis canicola* adhered to the intestine with penetration through the mucosa and partial penetration of the submucosa. (B) Higher magnification of grey rectangle in (A) showing the proboscis with visible hooks (H) embedded in the submucosa with associated inflammatory cells (black arrows). Bacterial colonies and fibrosis are evident at the leading edge of the parasite (white arrows). Photo credits Leslie Woods.

2012, the distribution of body condition classes was relatively constant, except for 2007, when the odds of higher condition were significantly lower compared with 2011 (odd ratio (OR): 0.43; 95% confidence interval (95% CI): 0.24–0.79) (Supplementary Fig. S3). The odds for foxes with high body condition were significantly lower than in 2011 in nine out of the 11 years in which the parasite has been detected on the island. These odds peaked between 2013 and 2017 (OR range: 0.01–0.08), decreasing slightly thereafter (OR range 2018–2022: 0.09–0.48), yet never returning to the levels observed before the emergence of the acanthocephalan parasite (Supplementary Fig. S2). Fox weight showed a similar trend to body condition, as in eight out of 11 years in which the parasite has been detected, the weight was significantly lower than in 2011 (Supplementary Table S2). Both the arrival of the acanthocephalan parasite and precipitation during the previous rainy season had a significant association with the trend of SMIF body condition (GLMM; Parasite arrival: $b = -1.1181$, S.E. = 0.2604, $P < 0.001$, Precipitation: $b = 0.0011$, S.E. = 0.0005, $P = 0.02$). However, the interaction of both variables was not significant and thus excluded from the best model (Supplementary Table S3). Parasite

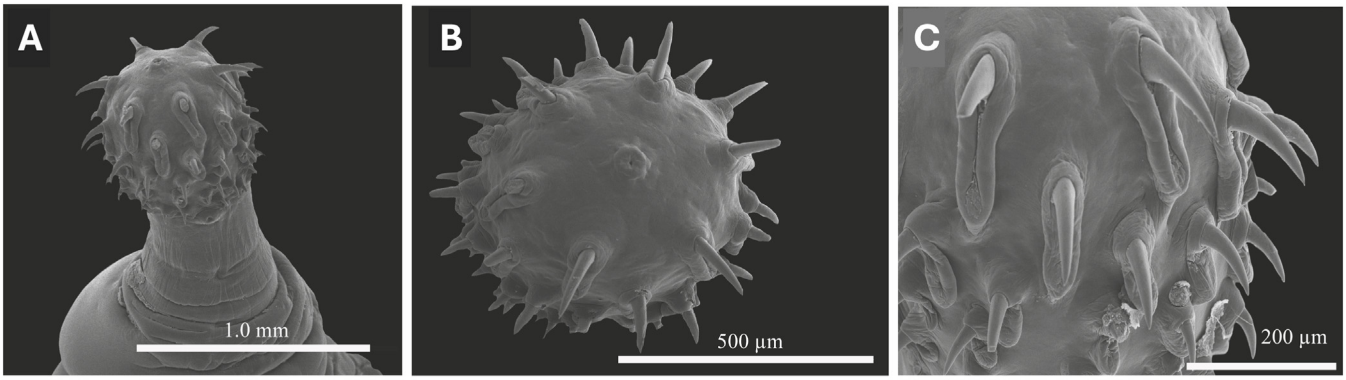

Fig. 3. Scanning electron micrograph of the acanthocephalan *Pachysentis canicola* from San Miguel Island fox (*Urocyon littoralis littoralis*). (A) Distinctive elongated neck and proboscis in an adult male, ventral view. (B) Proboscis, adult male horizontal view. (C) Hooks. Photo credits Martín García-Varela.i

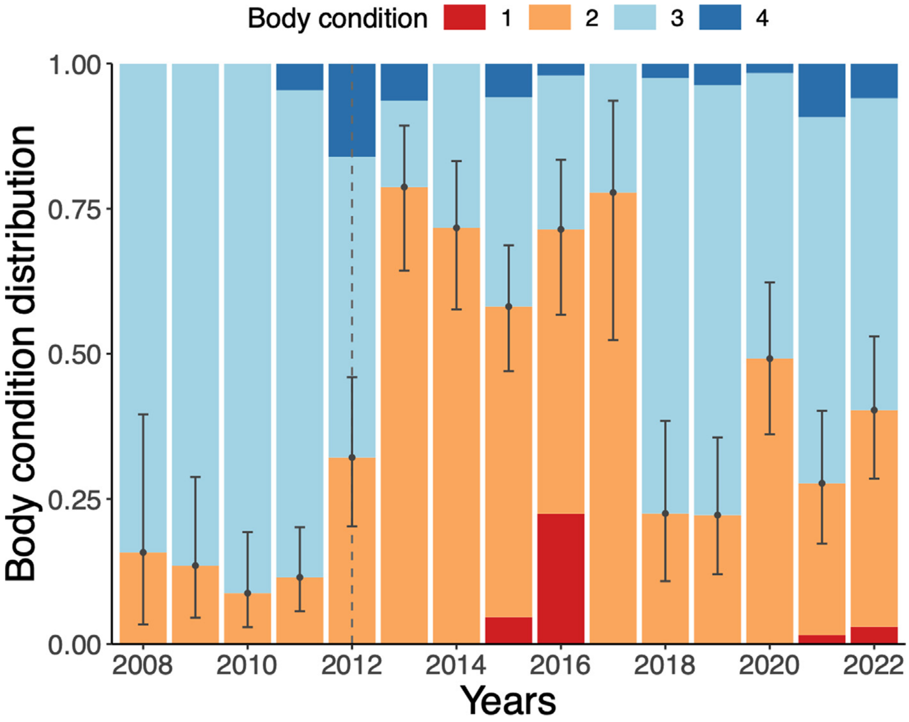

Fig. 4. Distribution of the body condition scores of San Miguel Island foxes (*Urocyon littoralis littoralis*) (SMIFs) between 2008 and 2022. Body condition scores range from 1 (bottom), indicating the worst condition, to 4 (top), indicating the best condition. The dashed line represents the year when the acanthocephalan parasite, Pachysentis canicola, was first detected in SMIFs. Points and associated error bars represent the proportion of foxes with body condition 2 or lower, and their respective binomial confidence intervals.

arrival was followed by a significant decrease in fox weight (GLMM; parasite arrival: $b = -0.1208$, S.E. = 0.0227, $P < 0.001$; sex (male): $b = 0.171$, S.E. = 0.026, $P < 0.001$), while precipitation and its interaction with parasite arrival were excluded from the best model (Supplementary Table S4). Considering the acanthocephalan emergence in 2012 as the "intervention" date indicated that the proportion of high body condition foxes (body conditions 3 and 4) diminished on average by 27% (23–30%) below expectations after 2012 ($P < 0.001$) (Figs. 4 and 5).

The survival rates of both pups and adult SMIFs declined after 2012 (Fig. 6). The very low survival rate of pups between 2014 and 2017 overlapped with a drought. Concurrently, the pup/adult ratio in SMIFs decreased after the parasite was identified on the island with its lowest level in 2014. Although pup survival partially rebounded after the drought ended in 2018, the post-2012 reduction in survival persisted.

4. Discussion

The acanthocephalan *P. canicola* has infected SMIFs since 2012, preceding a dramatic fox population decline occurring in 2014. Foxes with large numbers of acanthocephalans had enteritis and were emaciated. Survival declined, and captured foxes were more likely to be in poor body condition and lower weight after the parasite was first observed. In severe cases, this damage led to ulcerative enteritis, transmural necrosis and inflammation, peritonitis and death. Reduced health was also associated with drought. Our findings highlight the need to continue improving our understanding of the life history of *P. canicola* and the consequences of its infection in the hosts, while making efforts to prevent this parasite from invading other Channel Islands.

Pachysentis canicola is sufficiently generalist to infect SMIFs that have been separated from this mainland parasite for thousands of

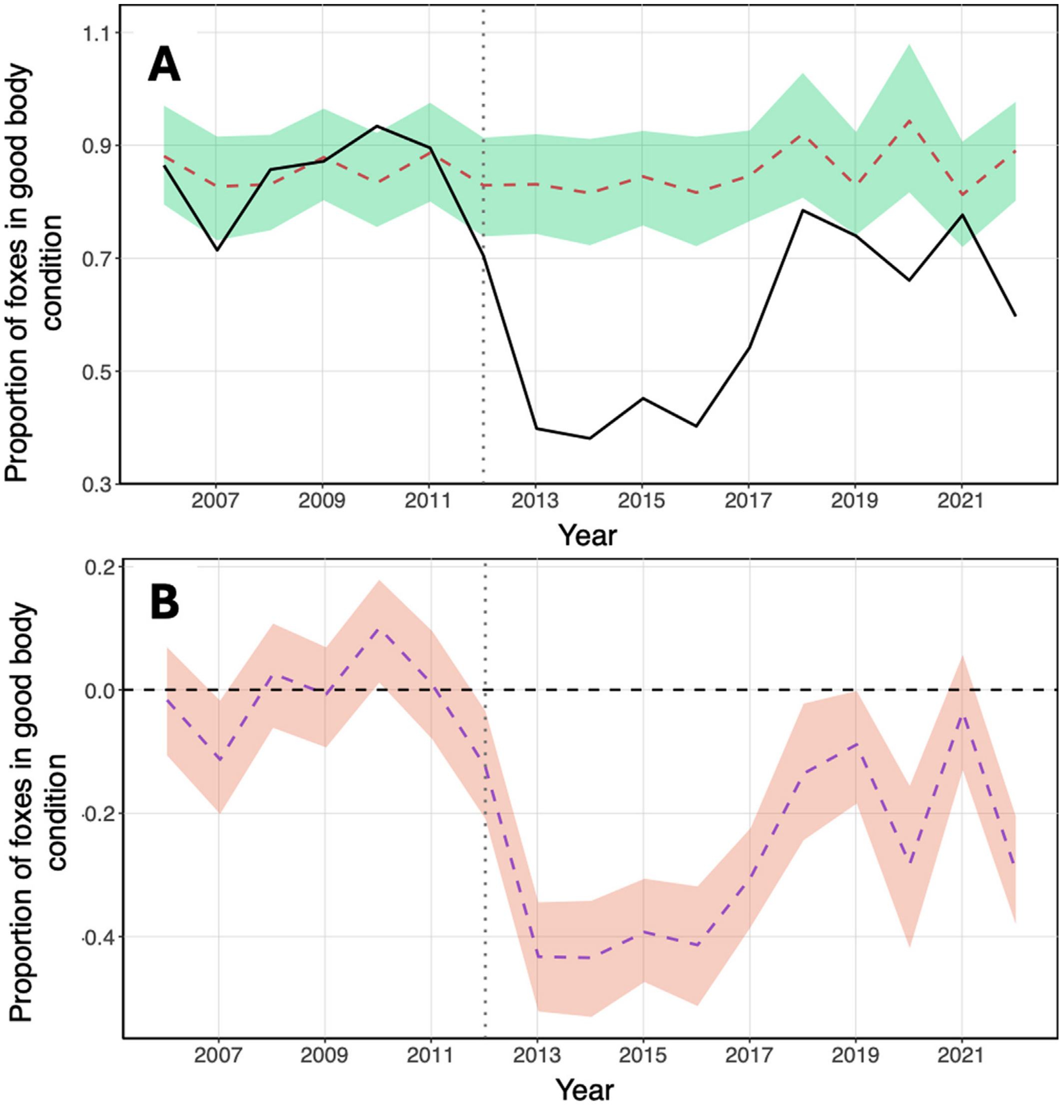

Fig. 5. Intervention analysis to explore the influence of *Pachysentis canicola* in the time series of San Miguel Island fox (*Urocyon littoralis littoralis*) (SMIFs) body condition between 2006 and 2022. The dotted vertical lines represent the year when the acanthocephalan parasite *P. canicola* was first detected in SMIFs, which determined the pre-and post-intervention period. (A) shows the original time series of SMIFs in high body condition (continuous line) and the counterfactual prediction ± 95% confidence interval of this proportion in the absence of the parasite (dashed line within shaded envelope). (B) The difference between the time series (data) and the predicted trend in the absence of the parasite (dashed line within shaded envelope representing ± 95% confidence interval). This represents an estimate of the causal effect of the parasite on the good body condition time series of SMIFs ($P < 0.01$).

years. *Pachysentis canicola* was first described by Meyer (1931) from an undetermined Brazilian canid. Subsequently, *P. canicola* has been reported primarily from the gray fox, *Urocyon cinereoargenteus,* and skunks, including the hog-nosed skunk, *Conepatus leuconotus*, eastern striped skunk, *Mephitis mephitis,* and western spotted skunk, *Spilogale gracilis*,(Van Cleave, 1953; Amin et al., 2022), but has also been reported from a coyote, *Canis latrans*, raccoon, *Procyon lotor*, ringtail, *Bassariscus astutus,* and maned wolf, *Chrysocyon brachyurus* (Amin et al., 2022). None of the alternate host groups occur on San Miguel Island, though a subspecies of the spotted skunk (*Spilogale gracilis amphiala*) occurs on nearby Santa Cruz and Santa Rosa Islands. Reports of *P. canicola* in the United States have been limited to Texas, Oklahoma, and Arizona (Neiswenter et al., 2006, Bolette 1997, Buechner 1944, Van Cleave 1953). The current study expands the geographic range and the SMIF represents a new host record for *P. canicola*.

To our knowledge, *P. canicola* does not yet occur on the other Channel Islands; thus efforts should be made to contain this parasite to San Miguel Island. During the captive reproduction program, fresh fecal samples of SMIFs were routinely analyzed for parasite egg counts, and the acanthocephalan parasite was never detected (Coonan and Rutz, 2001, 2002). Given that the recovery program did not move foxes or other final hosts between islands, the most likely way the acanthocephalan arrived on San Miguel Island is via an infected arthropod host accidentally transported by humans, perhaps hitch-hiking on gear, equipment, or supplies of campers or national park employees or, ironically, biologists involved in fox monitoring or captive breeding. This is also one way that the acanthocephalan might spread to nearby Santa Rosa or Santa Cruz Islands. If this were to occur, fox declines seem likely. Spillover to the endemic spotted skunk, a species of interest due to their limited range and low detection levels, and in which the consequences of infection are currently unknown, is also likely. Thus, identifying the acanthocephalan's intermediate host could help inform biosecurity protocols needed to reduce the risk that the parasite will spread to other island carnivore populations. Despite the many invertebrates dissected in our study, no intermediate stages of acanthocephalan parasites were observed. However, increasing

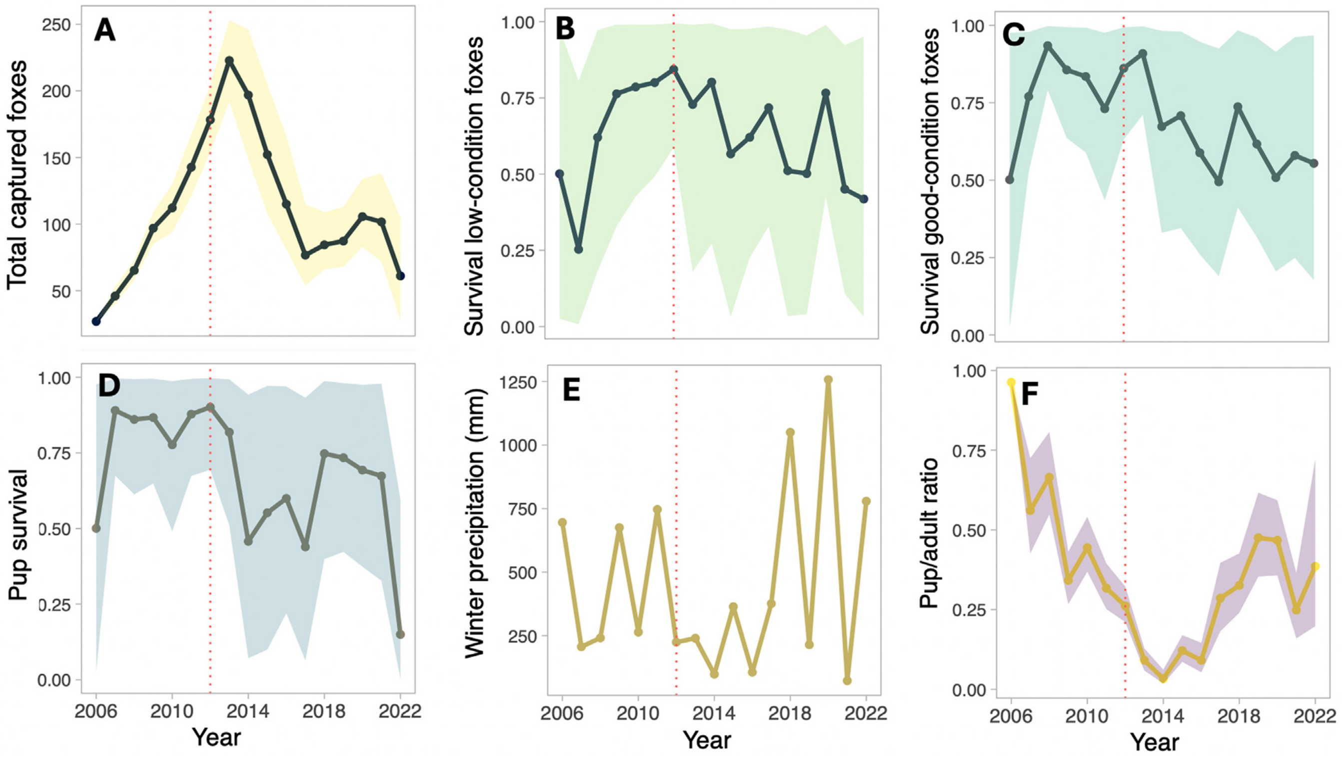

Fig. 6. Demographic parameters for San Miguel Island fox (*Urocyon littoralis littoralis*) between 2006 and 2022. (A-D, F) Using capture-recapture data and a Bayesian multistate Cormack-Joly-Seber (CSJ) capture-recapture model with data augmentation, temporal random effects to control for differences in capture efforts, and three demographic states: pups, adults in low body condition, and adults in high body condition. The shaded areas represent credible intervals. (E) Winter precipitation on San Miguel Island between 2006 and 2022. The dashed vertical line separates time periods before and after parasite detection.

the sampling effort in the more underrepresented groups could rule out those species with greater certainty. Because a comprehensive monthly parasitological survey of SMIF scat revealed an increased density of *P. canicola* eggs during warmer months (Childress, J.N. 2023. The Parasite Ecology of the San Miguel Island Fox, *Urocyon littoralis littoralis* (Doctoral dissertation). University of California, Santa Barbara, California, USA), additional invertebrate dissections conducted in these months might be needed, particularly for large orthopterans such as the Jerusalem cricket, *Stenopelmatus* spp. Furthermore, some reptile species (Bolette, 1997; Macedo et al., 2016) can act as paratenic hosts for *Pacysentis,* suggesting that foxes might become exposed to parasites by consuming these groups rather than arthropods. We could only dissect herpetofauna incidentally due to restrictions on the live take of these endemic vertebrates. Identifying the acantocephalan's life cycle remains a research priority.

The potential impact of *P. canicola* was obvious from necropsies. They attached deep into the fox intestinal mucosa, reaching the muscularis and, in some cases, going through the intestinal wall. It required the use of forceps and significant pulling force to separate individual parasites from the intestinal tissue. The diffusely thickened and flaccid intestines, necrosis, pleocellular inflammation, and fibrosis associated with *P. canicola* have been described in other perforating acanthocephalans (Bullock, 1963; McDonough and Gleason, 1981; Taraschewski, 2000; Feist and Longshaw, 2008). The histopathology of intestines of SMIF infected with *P. canicola* is similar to other perforating acanthocephalan species. Bacteria that colonize the space between the parasite and host intestine can lead to secondary infections (Tesana et al., 1982; Taraschewski, 2000) and intussusceptions. Subsequent peritonitis associated with intestinal perforation can lead to death (Stunkard, 1965; Zárate-Ramos et al., 2018). It is not surprising that this parasite might cause health problems in island foxes, particularly given that island hosts are often intolerant of parasites from which they have been isolated for generations (Lafferty et al., 2010). In addition, the genetic bottleneck resulting from the extreme population decline in the late 1990s before the captive breeding program could have impaired the immune response of foxes at the population level.

The necropsies found other parasites such as *Spirocerca* sp., *Calodium hepaticum*, the tapeworm *Mesocestoides corti*, the hookworm *Uncinaria stenocephala*, and the lungworm *Angiocaulus gubernaculatus* (Childress, 2023, doctoral dissertation, cited earlier), which can be considered core parasite fauna of the island fox. Some acute fox mortalities were attributed to colonic lesions caused by *Spirocerca* sp. (Coonan, 2003; Coonan et al., 2004). Most of these mortalities resulted from acute septicemia triggered by prolapsed rectum or transmural colitis secondary to high *Spirocerca* infestation. Although *U. stenocephala* is highly prevalent on the island and capable of producing pathogenic consequences in other canids (Seguel and Gottdenker, 2017), it does not seem to impact SMIF health significantly (Coonan et al., 2005). Finally, the lungworm *A. gubernaculatus* can cause extensive pulmonary lesions, including inflammation and pulmonary granulomas (Coonan et al., 2004); however, its overall pathogenicity remains largely unknown. The parasite diversity in San Miguel Island highlights the inherent difficulty of understanding the effect of a single parasite. Nevertheless, when taken together, our findings suggest that although some endemic parasite species such as *A. gubernaculatus* and *Spirocerca* sp., might have relevant pathological consequences and even cause mortality, these events seem to be sporadic compared with the consistent decrease in the overall health of SMIFs after *P. canicola* arrived.

Because mortality began before the drought (and continued after), we are confident that the initial effects attributed to the acanthocephalan were not caused by environmental stress. However, the environmental signal in fox mortalities adds to the concerns for management and recovery options. Environmental stress can affect pathogen development, persistence, and mortality while also affecting the physiological (e.g., immune) and behavioral responses of both hosts and vectors, thereby influencing disease outcomes such as transmission, intensity, and pathology (Lafferty and Holt, 2003). This phenomenon has been extensively documented in various host-parasite systems, encompassing both macroparasites (Cardon et al., 2011; Pontifes et al., 2022) and microparasites (Oppliger et al., 1998; Shvydka et al., 2020; Aleuy et al., 2022). Yet, the data suggest that drought effects were additive, not synergistic. We suspect the SMIF can persist with *P. canicola* when conditions are favorable or with drought when parasites are absent, but extra actions might be needed to protect the population against parasitism during drought or to alleviate drought effects to help offset impacts by parasites. It is important to consider the hypothesis that the acanthocephalan parasite may have been present on the island prior to 2012 but went undetected during earlier surveillance due to low parasite intensities. For instance, a change in the prey preferences of foxes, potentially increasing their exposure to the acanthocephalan intermediate host, could have led to an increase in parasite intensity. Such dietary shifts can result from significant environmental changes, such as the drought described in our research, or from more subtle, species-specific constraints that limit the availability of primary food sources, thereby compelling foxes to rely on alternative prey items.

Management options seem limited. To date, SMIFs have not been treated with antihelminthic drugs because there have not been clinical signs or demographic consequences attributable to parasites that would warrant such intense management actions. The efficacy of pharmacological treatment of acanthocephalan parasites is often unknown on a species-specific basis and has a variable and often poor efficacy (Zárate-Ramos et al., 2018). Although new evidence shows promising results using bioinformatics tools to reduce the time and cost of developing new treatment strategies against acanthocephalan parasites, further research is needed (Schmidt et al., 2022). Another option that is not necessarily less complicated would be to control the invertebrate(s) that serve as an intermediate host of the parasite. This might be tenable if the arthropod was one of many non-endemic species present on the island. Thus, preventing the spread of the acanthocephalan to other Channel Islands could be considered.

To conclude, we have identified the acanthocephalan parasite *P. canicola* in SMIFs and described its impact on fox health together with the potential for population-level impacts. Heavy infections with *P. canicola* are common and can cause severe damage to intestinal tissues and systemic consequences such as transmural intestinal necrosis, peritonitis, and death. *Pachysentis canicola* was first identified during necropsies of SMIFs in 2012. Subsequently, both body condition and weight decreased in pups and adults while mortality, particularly in pups, increased. San Miguel Island is the smallest and least diverse of the Channel Islands supporting a fox population, making the SMIF inherently more vulnerable to stochastic events and *P. canicola* might exacerbate this risk. Altogether, these results suggest the need for increased biosecurity within the Channel Islands National Park, and more research to understand the biology of *P. canicola* and its effects on SMIF population dynamics.

CRediT authorship contribution statement

O. Alejandro Aleuy: Writing – review & editing, Writing – original draft, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Leslie W. Woods:** Writing – review & editing, Writing – original draft, Investigation, Formal analysis, Data curation, Conceptualization. **Benjamin J. Padilla:** Writing – review & editing, Investigation, Formal analysis, Conceptualization. **Dennis Richardson:** Writing – review & editing, Investigation, Formal analysis, Data curation, Conceptualization. **Juliann T. Schamel:** Writing – review & editing, Methodology, Investigation, Data curation, Conceptualization. **Stacy Baker:** Writing – review & editing, Investigation, Data curation, Conceptualization. **Martín García-Varela:** Writing – review & editing, Investigation, Formal analysis, Data curation. **Charlotte Hammond:** Writing – review & editing, Investigation, Formal analysis, Conceptualization. **Sarah P. Lawson:** Writing – review & editing, Investigation, Formal analysis, Conceptualization. **Jasmine N. Childress:** Writing – review & editing, Formal analysis, Data curation. **Jason Rohr:** Writing – review & editing, Supervision, Methodology, Investigation, Funding acquisition, Conceptualization. **Kevin D. Lafferty:** Writing – review & editing, Writing – original draft, Supervision, Methodology, Investigation, Data curation, Conceptualization.

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Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ijpara.2024.09.003.

References

Aleuy, O.A., Anholt, M., Orsel, K., Mavrot, F., Gagnon, C.A., Beckmen, K., Côté, S.D., Cuyler, C., Dobson, A., Elkin, B., Leclerc, L.M., Taillon, J., Kutz, S., 2022. Association of Environmental Factors with Seasonal Intensity of *Erysipelothrix rhusiopathiae* Seropositivity among Arctic Caribou. Emerg. Infect. Dis. 28, 1650–1658.

Amin, O.M., Chaudhary, A., Heckmann, R.A., Swenson, J., Singh, H.S., 2022. Redescription and Molecular Characterization of *Pachysentis canicola* Meyer, 1931 (Acanthocephala: Oligacanthorhynchidae) from the Maned Wolf, *Chrysocyon brachyurus* (Illiger, 1815) in Texas. Acta Parasitol. 67, 275–287.

Armstrong, B.G., Sloan, M., 1989. Ordinal regression models for epidemiologic data. Am. J. Epidemiol. 129, 191–204.

Bakker, V.J., Doak, D.F., Ferrara, F.J., 2021. Understanding extinction risk and resilience in an extremely small population facing climate and ecosystem change. Ecosphere 12, e03724.

Boitani, L., Asa, C., Moehrenschlager, A., 2004. Conservation tools for Canids. In: Macdonald, D.W., Sillero-Zubiri, C. (Eds.), The Biology and Conservation of Wild Canids. Oxford University Press, Oxford, UK, pp. 143–161.

Bolette, D.P., 1997. First record of *Pachysentis canicola* (Acanthocephala: Oligacanthorhynchida) and the occurrence of *Mesocestoides* sp. tetrathyridia (Cestoidea:Cyclophyllidea) in the western diamondback rattlesnake, *Crotalus atrox* (Serpentes:Viperidae). J. Parasitol. 83, 751–752.

Box, G.E.P., Tiao, G.C., 1975. Intervention analysis with applications to economic and environmental problems. J. Am. Stat. Assoc. 70, 70–79.

Brodersen, K.H., Gallusser, F., Koehler, J., Remy, N., Scott, S.L., 2014. Inferring causal impact using Bayesian structural time-series models. Ann. Appl. Stat. 9, 247–274.

Brooks, M.E., Kristensen, K., van Benthem, K.J., Magnusson, A., Berg, C.W., Nielsen, A., Skaug, H.J., Maechler, M., Bolker, B.M., 2017. glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. R J. 9, 378–400.

Buechner, H.K., 1944. Helminth parasites of the Gray Fox. J. Mammal. 25, 185–188.

Bullock, W.L., 1963. Intestinal histology of some salmonid fishes with particular reference to the histopthology of acanthocephalan infections. J. Morphol. 112, 23–44.

Cardon, M., Loot, G., Grenouillet, G., Blanchet, S., 2011. Host characteristics and environmental factors differentially drive the burden and pathogenicity of an ectoparasite: a multilevel causal analysis. J. Anim. Ecol. 80, 657–667.

Coonan, TJ., Rutz, K., 2001. Island Fox Captive Breeding Program 1999–2000 Annual Report. National Park Service, Channel Islands National Park.

Coonan, T.J., Rutz, K., 2002. Island Fox Captive Breeding Program 2001 Annual Report. National Park Service, Channel Islands National Park.

Coonan, T.J, Rutz, K.A., McCurdy, K., Garcelon, D.K., Latta, B.C., Munson, L., 2004. Island Fox Recovery Program 2003 Annual Report. National Park Service, Channel Islands National Park.

Coonan, T.J., Schwemm, C.A., Roemer, G.W., Garcelon, D.K., Munson, L., 2005. Decline of an island fox subspecies to near extinction. Southwest. Nat. 50, 32–41.

Coonan, T.J., 2003. Recovery strategy for island foxes (*Urocyon littoralis*) on the northern Channel Islands. National Park Service. Available from https://corpora.tika.apache.org/base/docs/govdocs1/271/271872.pdf (accessed July 5, 2023).

de Valpine, P., Turek, D., Paciorek, C.J., Anderson-Bergman, C., Lang, D.T., Bodik, R., 2017. Programming with models: writing statistical algorithms for general model structures with NIMBLE. J. Comput. Graph. Stat. 26, 403–413.

Dillon, A., Shaskey, L.E., 2022. Island Fox Recovery Program: Channel Islands National Park Population Trends (2006-2016) and Recovery Report. U.S. Department of the Interior, National Park Service, Natural Resource Stewardship and Science, USA.

Feist, S.W., Longshaw, M., 2008. Histopathology of fish parasite infections - importance for populations. J. Fish Biol. 73, 2143–2160.

Folmer, O., Black, M., Hoeh, W., Lutz, R., Vrijenhoek, R., 1994. DNA primers for amplification of mitochondrial cytochrome c oxidase subunit I from diverse metazoan invertebrates. Mol. Marine Biol. Biotechnol. 3, 294–299.

Galazzo, D.E., Dayanandan, S., Marcogliese, D.J., 2002. Molecular systematics of some North American species of *Diplostomum* (Digenea) based on rDNA-sequence data and comparisons with European congeners Canadian. Journal of Zoology 80, 2207–2217.

Gelman, A., Rubin, D.B., 1992. Inference from iterative simulation using multiple sequences. Stat. Sci. 7, 457–472.

Ginsberg, J.R., 1994. Captive breeding, reintroduction and the conservation of canids. In: Olney, P.J.S., Mace, G.M., Feistner, A.T.C. (Eds.), Creative Conservation: Interactive Management of Wild and Captive Animals. Springer, Netherlands, Dordrecht, pp. 365–383.

Gomes, A.P.N., Olifiers, N., Souza, J.G.R., Barbosa, H.S., D'Andrea, P.S., Maldonado, A., 2015. A new acanthocephalan species (Archiacanthocephala: Oligacanthorhynchidae) from the crab-eating fox (*Cerdocyon thous*) in the Brazilian pantanal wetlands. J. Parasitol. 101, 74–80.

Kennedy, C.R., 2006. Ecology of the Acanthocephala. Cambridge University Press, Cambridge, UK.

Lafferty, K.D., Holt, R.D., 2003. How should environmental stress affect the population dynamics of disease? Ecol. Lett. 6, 654–664.

Lafferty, K.D., Torchin, M.E., Kuris., A.M., 2010. The geography of host parasite invasions. In: Morand, S., Krasnov, B. (Eds.), The Biogeography of Host-Parasite Interactions. Oxford University Press, Oxford, England.

Light, J.E., Siddall, M.E., 1999. Phylogeny of the leech family Glossiphoniidae based on mitochondrial gene sequences and morphological data. J. Parasitol. 85, 815–823.

Macedo, L.C., Melo, F., Ávila-Pires, T.C.S., Giese, E.G., dos Santos, J.N., 2016. Acanthocephala Larvae parasitizing *Ameiva ameiva ameiva* (Linnaeus, 1758) (Squamata: Teiidae). Revista Brasileira de Parasitologia Veterinaria 25, 119–123.

McDonough, J.M., Gleason, L.N., 1981. Histopathology in the rainbow darter, *Etheostoma caeruleum*, resulting from infections with the Acanthocephalans, *Pomphorhynchus bulbocolli* and *Acanthocephalus dirus*. J. Parasitol. 67, 403–409.

Neiswenter, S.A., Pence, D.B., Dowler, R.C., 2006. Helminths of sympatric striped, hog-nosed, and spotted skunks in west-central Texas. J. Wildl. Dis. 42, 511–517.

Oppliger, A., Clobert, J., Lecomte, J., Lorenzon, P., Boudjemadi, K., John-Alder, H.B., 1998. Environmental stress increases the prevalence and intensity of blood parasite infection in the common lizard Lacerta vivipara. Ecology 1, 129–138.

Pleijel, F., Jondelius, U., Norlinder, E., Nygren, A., Oxelman, B., Schander, C., Sundberg, P., Thollesson, M., 2008. Phylogenies without roots? A plea for the use of vouchers in molecular phylogenetic studies. Mol. Phylogenet. Evol. 48, 369–371.

Pontifes, P.A., Fernández-González, A., García-Peña, G.E., Roche, B., Suzán, G., 2022. Drivers of flea abundance in wild rodents across local and regional scales in the Chihuahuan Desert, northwestern Mexico. Ecosphere 13, e4013.

Prendini, L., Weygoldt, P., 2005. Systematics of the *Damon variegatus* group of African whip spiders (Chelicerata: Amblypygi): evidence from behaviour, morphology and DNA. Organisms, Diversity and Evolution 5, 203–236.

Richardson, D.J., 2006. Life Cycle of *Oligacanthorhynchus tortuosa* (Oligacanthorhynchidae), an Acanthocephalan of the Virginia Opossum (*Didelphis virginiana*). Comp. Parasitol. 73, 1–6.

Richardson, D.J., Barger, M.A., 2006. Redescription of *Oligacanthorhynchus major* (Machado-Filho, 1963) Schmidt, 1972 (Acanthocephala: Oligacanthorhynchidae) from the white-lipped peccary (*Tayassu pecari*) in Bolivia. Comp. Parasitol. 73, 157–160.

Richardson, D.J., Moser, W.E., Hammond, C.I., Shevchenko, A.C., Lazo-Wasem, E., 2010. New Geographic Distribution Records and Host Specificity of *Placobdella ali* (Hirudinida: Glossiphoniidae). Comp. Parasitol. 77, 202–206.

Roemer, G.W., Coonan, T.J., Garcelon, D.K., Bascompte, J., Laughrin, L., 2001. Feral pigs facilitate hyperpredation by golden eagles and indirectly cause the decline of the island fox. Anim. Conserv. Forum 4, 307–318.

Roemer, G.W., Donlan, C.J., Courchamp, F., 2002. Golden eagles, feral pigs, and insular carnivores: how exotic species turn native predators into prey. Proc. Nat. Acad. Sci. USA 99, 791–796.

Royle, J.A., Dorazio, R.M., 2012. Parameter-expanded data augmentation for Bayesian analysis of capture–recapture models. J. Ornithol. 152, 521–537.

Rubin, E.S., Bakker, V.J., Efford, M.G., Cohen, B.S., Stallcup, J.A., Spencer, W.D., Morrison, S.A., 2007. A population monitoring framework for five subspecies of island fox (*Urocyon littoralis*). Conservation Biology Institute and The Nature Conservancy for the Recovery Coordination Group of the Integrated Recovery Team. California, USA.

Saari, S., Näreaho, A., Nikander, S., 2019. Chapter 6 - Acantocephala (Thorny-Headed Worms). In: Saari, S., Näreaho, A., Nikander, S. (Eds.), Canine Parasites and Parasitic Diseases. Academic Press, USA, pp. 151–155.

Sanil, N.K., Asokan, P.K., John, L., Vijayan, K.K., 2011. Pathological manifestations of the acanthocephalan parasite, *Tenuiproboscis* sp. in the mangrove red snapper (*Lutjanus argentimaculatus*) (Forsskål, 1775), a candidate species for aquaculture from Southern India. Aquaculture 310, 259–266.

Schmidt, G.D., Nickol, B.B., 1985. Development and life cycles. In: Crompton, D.W., Nickol, B,B, (ed), Biology of Acanthocephala, Cambridge University Press, UK, pp. 273–305.

Schmidt, H., Mauer, K., Glaser, M., Dezfuli, B.S., Hellmann, S.L., Silva Gomes, A.L., Butter, F., Wade, R.C., Hankeln, T., Herlyn, H., 2022. Identification of antiparasitic drug targets using a multi-omics workflow in the acanthocephalan model. BMC Genomics 23, 677.

Seguel, M., Gottdenker, N., 2017. The diversity and impact of hookworm infections in wildlife. Int. J. Parasitol. Parasites Wildl. 6, 177–194.

Shvydka, S., Cadarso-Suárez, C., Ballová, D., Sarabeev, V., 2020. Patterns of monogenean abundance in native and invasive populations of *Planiliza haematocheila* (Teleostei: Mugilidae): interactions between climate and host defence mechanisms explain parasite release. Int. J. Parasitol. 50, 1023–1031.

Stunkard, H.W., 1965. New intermediate hosts in the life cycle of *Prosthenorchis elegans* (Diesing, 1851), an acanthocephalan parasite of primates. J. Parasitol. 51, 645–649.

Suzuki, N., Hoshino, K., Murakami, K., Takeyama, H., 2008. Molecular diet analysis of phyllosoma larvae of the Japanese spiny lobster *Palinurus japonicus* (Decapoda: Crustacea). Marine Biotechnology 10, 49–55.

Taraschewski, H., 2000. Host-parasite interactions in Acanthocephala: a morphological approach. Adv. Parasitol. 46, 1–179.

Taylor, M.A., Coop, R.L., Wall, R.L., 2007. Veterinary Parasitology. Blackwell, UK.

Tesana, S., Mitrchai, J., Chunsuttwat, S., 1982. Acute abdominal pain due to *Macracanthorhynchus hirudinaceus* infection: a case report. Southeast Asian. J. Trop. Med. Public Health 13, 262–264.

Van Cleave, H.J., 1953. Acanthocephala of North American Mammals. Univ Illinois Press, Urbana, USA.

Wayne, R.K., George, S.B., Gilbert, D., Collins, P.W., Kovach, S.D., Girman, D., Lehman, N., 1991. A morphologic and genetic study of the island fox, *Urocyon littoralis*. Evolution 45, 1849–1868.

Zárate-Ramos, J.J., Gómez-Garza, M.A., Rodríguez-Tovar, L.E., Escareño, J.H., Contreras-Lozano, J.A., 2018. An Alternative Treatment Against Acanthocephala (*Prosthenorchis elegans*) in Captive Squirrel Monkeys (*Saimiri sciureus*) in Mexico. J. Parasitol. 104, 574–575.