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Research Article

A Preliminary Study Assessing Risk to Tasmanian Devils From Poisoning for Red Foxes

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ABSTRACT The recent introduction of red foxes (*Vulpes vulpes*) to Australia's island state of Tasmania represents a major threat to native fauna. In response, the Tasmanian government has begun a fox eradication program using Foxoff®, a bait containing the poison sodium monofluoroacetate (commonly known as 1080). The bait is potentially attractive to native Tasmanian carnivores as well as to foxes. Of particular concern is the endangered Tasmanian devil (*Sarcophilus harrisii*), which is already at risk from an emergent infectious disease, devil facial tumor disease (DFTD). In both a captive and a field study using non-toxic Foxoff bait, we assessed bait palatability and possible effects of demographics, hunger level, bait age, and bait burial method on the likelihood of bait uptake by Tasmanian devils. Captive devils showed varying interest in the bait, but wild devils appeared to find it uniformly palatable. In the captive study, males and younger, captive-born animals were more likely to excavate and remove bait. Subterranean burial at 15 cm was the most effective deterrent to bait excavation; effectiveness decreased at shallower depths and with surface-level bait buried beneath soil mounds. Our findings suggest that the current fox-baiting campaign may negatively impact individual devils. More extensive study is necessary to assess potential risk at the population level.

KEY WORDS bait palatability, bait uptake, poisoning, red fox, remote photography, *Sarcophilus harrisii*, sodium monofluoroacetate (1080), Tasmania, Tasmanian devil, *Vulpes vulpes*.

The red fox (*Vulpes vulpes*; hereafter fox) is the world's most widespread terrestrial wild carnivore (Larivière and Pasitschniak-Arts 1996, Macdonald and Reynolds 2004). The species was first successfully introduced to Australia in the 1870s. Its current distribution is >4 million km^2, including all of Australia except tropical regions (Saunders et al. 1995, 2006). Foxes have had a devastating impact on native Australian fauna, particularly on small and medium-sized mammals. Predation by foxes contributed to total extinction of several mammal species, as well as to mainland extinction of several species that survive only in relictual populations on small offshore islands or in Tasmania (Short and Smith 1994). Examples of total extinctions include the toolache wallaby (*Macropus greyi*; Australian Mammal Assessment Workshop 2008*b*), crescent nail-tail wallaby (*Onychogalea lunata*; Burbidge and Johnson 2008), desert rat-kangaroo (*Caloprymnus campestris*; Australian Mammal Assessment Workshop 2008*a*), desert bandicoot (*Perameles eremiana*; Burbidge et al. 2008*a*), and lesser bilby (*Macrotis leucura*; Burbidge et al. 2008*b*). Examples of mainland extinctions include the rufous hare-wallaby (*Lagorchestes hirsutus*; Richards et al. 2008*b*), banded hare-wallaby (*Lagostrophus fasciatus*; Richards et al. 2008*a*), Tasmanian pademelon (*Thylogale billardierii*; Menkhorst and Denny 2008), western barred bandicoot (*Perameles bougainville*; Friend and Richards 2008), and greater stick-nest rat (*Leporillus conditor*; Morris and Copley 2008). The Australian government has identified 62 species on the mainland that are at particular risk from foxes. The list includes 34 vulnerable, 23 endangered, and 5 critically endangered species (Australian Department of the Environment, Water, Heritage and the Arts 2008).

There have been infrequent incursions of foxes into Tasmania since early European colonization, but the species did not become established. However, recent evidence indicates that the fox was introduced to Tasmania again in the last decade, with reports becoming more frequent and widespread (Saunders et al. 2006). Surveillance through genotyping of scat has identified 56 fox scats from ≥15 individual animals (Tasmanian Department of Primary Industries, Parks, Water and the Environment 2010). Should the fox become established in the state, it would likely have an environmental impact comparable to that on the mainland.

Burbidge and McKenzie (1989) determined that species with masses between 35 g and 5.5 kg are particularly susceptible to predation by foxes. Tasmania has 78 terrestrial vertebrate species in this weight range, including 12 threatened, 16 declining, and 34 locally range-restricted species (Saunders et al. 2006). Among the species at risk from foxes

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are the state's 3 large dasyurids: the Tasmanian devil (*Sarcophilus harrisii*; hereafter devil), spotted-tailed quoll (*Dasyurus maculatus*), and eastern quoll (*D. viverrinus*); the latter is of particular concern because foxes were implicated in its extinction on the mainland (Jones and Rose 2001, Saunders et al. 2006).

The potential interplay between foxes and Tasmanian devils deserves special mention. Some researchers have speculated that devils helped to prevent fox establishment during previous incursions in Tasmania (Bloomfield et al. 2005, Saunders et al. 2006, Jones et al. 2007). If that is the case, declines in devil numbers as a result of DFTD (Hawkins et al. 2006) may allow foxes to establish permanently. An established fox population could further threaten the devil, through both competition and predation on juvenile devils (Saunders et al. 1995).

Poisoning is the most effective fox-control method, and the only method suitable for control at the broad scale needed in Tasmania (Gentle 2005, Saunders et al. 2006). The Tasmanian government has implemented a poison-baiting regime aimed at eradicating the foxes currently in Tasmania before the species becomes irremediably established (Mooney et al. 2005). The program uses primarily Foxoff® (Animal Control Technologies, Melbourne, VIC, Australia), a processed meat-based bait containing sodium monofluoroacetate (1080) poison. Most Australian native species have a naturally higher resistance to 1080 than do introduced species, but bait consumption trials with non-toxic Foxoff bait suggest that spotted-tailed and eastern quolls are capable of consuming enough bait to ingest a theoretically lethal dose (McIlroy 1986, Belcher 1998, Glen and Dickman 2003). No such studies have been published for the Tasmanian devil.

Field studies assessing the potential impact of Foxoff baiting campaigns on spotted-tailed quolls on the mainland have generally found low individual mortality and no negative impact at the population level (Körtner et al. 2003, Körtner and Watson 2005, Glen et al. 2007, Körtner 2007). However, Belcher (2003) identified a correlation between Foxoff poisoning campaigns and declines in spotted-tailed quoll populations. Because fox baiting has historically been unnecessary in Tasmania, little field research has been conducted to assess the risk that Foxoff might pose to the state's endemic large dasyurids (the Tasmanian devil and the eastern quoll).

Before starting its fox-baiting campaign, the Tasmanian government conducted pilot studies of potential bait uptake by a wide variety of native species. Several bait types, including the non-toxic version of Foxoff, were equally palatable to wildlife (species undetermined), with >90% of surface-laid baits removed within 1 week. Only 10–15% of baits buried at 15 cm were taken during the same period. When operational poisoning began—using dried kangaroo meat baits buried at 15 cm—only 2–4% of baits were taken. Capture-mark-recapture studies did not yield enough data to determine population effects on either quoll species, and the impact of DFTD was a confounding factor that made it impossible to identify population effects on devils. But recapture rates for individuals were in the expected range, suggesting the impact might be limited (Mooney et al. 2005).

Baiting protocols have changed since those studies. Burial depth was reduced to 5 cm, then changed to 8–10 cm, and Foxoff instead of dried kangaroo meat is now the primary bait used (N. Mooney, Tasmanian Department of Primary Industries, Parks, Water and Environment, personal communication). For that reason, we chose to study Tasmanian devils' response to Foxoff. Specifically, we wanted to assess whether the bait is palatable to devils and to investigate the possible influence of demographic factors, hunger level, bait age, and bait burial method on bait uptake.

STUDY AREA

Captive Study

Study animals were housed in a lightly forested, off-exhibit area of the Australian Reptile Park, a private facility located on the Central Coast of New South Wales, eastern Australia (33°25′5″ S, 151°16′38″ E). The park was a participant in Project Ark, a captive-breeding program intended to build an insurance population of devils as a conservation strategy in response to DFTD.

Animals were held in 50–60 m^2 enclosures constructed of corrugated metal walls ≥1.5 m high and heavy-duty steel mesh underlying the substrate to prevent escape by digging. Substrate was shallow (<5 cm) and consisted of soil, mulch, and leaf litter. About 25% of the area of each enclosure was built up into one or more earth mounds, in which were buried plywood boxes and sections of hollow log for use as dens. Earth mounds were partially vegetated, and cut eucalyptus branches provided additional cover. All enclosures had an area shaded by shade cloth.

Field Study

We worked in Narawntapu National Park, formerly known as Asbestos Range National Park, on the central north coast of Tasmania (41°07′58″ S, 146°39′24″ E). Elevation ranged from 0 to 392 m above sea level. Vegetation communities included coastal heathland, dry sclerophyll forest, grassland, and salt marsh. The predominant substrate was a loose, sandy soil.

The site had high concentrations of common wombat (*Vombatus ursinus*), Forester kangaroo (*Macropus giganteus*), red-necked wallaby (*M. rufogriseus*), and Tasmanian pademelon (*Thylogale billardierii*), which in turn supported a large devil population. The park was apparently free of DFTD, although the disease had recently been detected just outside the park (R. Hamede, University of Tasmania, personal communication).

The Asbestos Range bisects the park and may have served as a barrier to easy movement by Tasmanian devils between the eastern and western sections of the park. The western section was more developed and more frequently visited, whereas the eastern section was mostly off-limits to public vehicular access.

METHODS

We performed our research in accordance with the guidelines of, and with approval of, the animal ethics committees of the Tasmanian Department of Primary Industries, Parks, Water and the Environment (approval number 26/2007–09) and the University of Sydney. Both institutions follow the Australian Code of Practice for the Care and Use of Animals for Scientific Purposes (Australian National Health and Medical Research Council 2004). We conducted our fieldwork at Narawntapu National Park under permit from the Tasmanian National Parks and Wildlife Service.

Foxoff bait is the most common mechanism for delivering 1080 to foxes in Australia (Gentle 2005). Available in both toxic and non-toxic versions, it is a processed meat-based bait, measuring approximately 3 cm × 3 cm × 3 cm and weighing approximately 35 g. The toxic version contains 3 mg of 1080 per bait. We used the non-toxic bait in our research.

Captive Study

We used 11 of Australian Reptile Park's 28 Tasmanian devils, excluding animals in quarantine, those housed in communal enclosures or rotated between exhibit and off-exhibit areas, and juveniles being raised by hand. Study animals were all adults, 7 females and 4 males, aged either 2 years or 4 years. All 2-year-old animals were born in captivity; all 4-year-olds were wild-caught. One 4-year-old female had a 7-month-old young at foot.

During the study, zookeepers fed animals a regular diet of fresh kangaroo meat. The weekly dietary regimen was 1 day of an 800-g portion, 4 days of a 500-g portion, 1 day of a 250-g portion, and 1 starve day on which the animals received no food. Varying daily food quantity simulated to some degree the natural fluctuations in food availability that devils might be expected to experience in the wild. Feeding took place in late afternoon. Water was available ad libitum. Park staff cleaned enclosures daily, removing scats as well as bones and any uneaten meat from the previous day's feeding.

Because of the steel mesh underlying the substrate, subterranean burial of bait was impossible. Instead, we assessed devils' response to bait placed at surface level and covered with a mound of river sand. To gather further information about the palatability of bait to devils, we also placed baits at surface level without sand coverage. We conducted the study over 2 non-consecutive periods in December 2007 and January 2008. We studied each animal for 9 days.

We mapped each animal's enclosure, dividing the area available for bait placement (i.e., the area exclusive of the earth mounds) into 9 numbered sectors of equal size. On the first day, we placed 1 Foxoff bait at surface level in a randomly assigned sector, covering it with leaf litter to prevent its discovery by corvid birds. We placed another bait in a second randomly assigned sector and covered it with a mound of river sand. Mounds were 25 cm in diameter and either 15 cm, 20 cm, or 25 cm high. We assigned mound height randomly. Every enclosure received each height on 3 of the 9 days. As a control to determine any effect of the presence of mounds per se, we also constructed an unbaited mound of the same height in a third randomly assigned sector.

On each subsequent day, we recorded the uncovering of surface-level bait, excavation of either mound, and removal of either bait. We considered any evidence of deliberate digging of a mound to qualify as excavation. Either the complete absence of a bait or any reduction in bait size qualified as removal. We then removed the 2 mounds (or their remnants), taking care to segregate the sand used in baited and unbaited mounds. We discarded any partially eaten bait but reused wholly uneaten bait. Finally, we repeated the bait placement and mound-building process, using new random assignments of sector and mound height. We reused sand from the previous day's mounds for the new day's mounds.

Field Study

We studied the eastern and western sections of the park for 8 nights each. In each section we set up 16 observation stations that included a baited and a control (unbaited) treatment. In the western section of the park, where the devil population was well studied, we chose station locations based on rates of past trapping success (R. Hamede, personal communication). In the eastern section, where such data were unavailable, we spaced observation stations evenly, at an interval of approximately 0.6 km, near the only 4-wheel-drive track, which was closed to public vehicular access. In both sections, we situated the stations in dry watercourses, along well-worn animal trails, or at devil latrine sites, all of which have contributed to higher trapping success rates in past studies (C. Hawkins, Tasmanian Department of Primary Industries, Parks, Water and Environment, personal communication). Because we sought to maximize devil visitation to observation stations, spatial randomness was not a goal.

The 2 phases took place over 18 consecutive days in January–February 2008. On the first day of each phase, we dug 2 square holes about 5 m apart at each observation station. Holes measured 10 cm × 10 cm and were 15 cm deep. One hole was the treatment (baited) and the other the control (unbaited). For treatment holes, we randomly assigned bait placement from among 4 options: 1) at surface level and covered by a mound of local sand; 2) 5 cm below the surface; 3) 10 cm below the surface; and 4) 15 cm below the surface. We designed our randomization matrix so that each observation station received each treatment on 2 of the 8 nights, and each treatment occurred at 4 observation stations per night. Due to human error, 1 day of the western phase had 5 stations with the 10-cm treatment and 3 with the mound treatment, rather than 4 of each.

For each treatment hole, we backfilled the hole with local sand to the depth necessary to achieve the assigned bait position, placed the bait, and backfilled the rest of the hole. For stations assigned the mound treatment, we backfilled the hole completely, placed the bait, and covered it with a mound of local sand 25 cm in diameter and 15 cm high. For each control hole, we backfilled the hole completely with sand and (where needed) constructed a similar sand mound.

We positioned a purpose-built infrared sensor (designed and constructed by J. Wiersma, Tasmanian Forest Practices Authority) housed in a Pelican 1010 microcase (Pelican Products, Torrance, CA) approximately 50 cm above each hole, using a metal bracket attached to a plastic stake. When the sensor was in place, we laid down a thin layer of local sand and smoothed it to form a pad 50 cm in diameter, to detect spoor of any animal that approached the hole or mound; this sand pad served as a backup in the event of camera malfunction, which occurred occasionally. Finally, we positioned a Pentax 33WR digital camera (Hoya Corporation, Tokyo, Japan) housed in a Seahorse SE120 waterproof case (Armored Group Inc., North Hollywood, CA) at surface level, approximately 75 cm from the sensor, secured to an aluminum stake. Cameras responded to a signal from the remote sensor and could take a photograph every 15–20 sec. The sensor was calibrated so that the camera took photographs only at night.

On subsequent days, we visited each observation station and recorded any evidence of excavation or bait removal, checked cameras and downloaded any photographs, and replaced depleted camera and sensor battery packs as needed. If a camera had failed to take photographs but there was evidence of visitation (either spoor or signs of excavation), we photographed the spoor or signs and (where possible) identified the species. When we had recorded the previous night's visitation and removal evidence, we prepared the observation station for the next night according to the same protocol. If the bait remained, we excavated and reused it. To reduce the potential effect of human scent, we wore latex gloves when handling bait and setting up and visiting observation stations.

We reviewed several thousand photographs, both from remote cameras and those we took of disturbed sand pads, to determine which species and how many individuals had visited each observation station on each night. When we could confirm visitation from remote camera photographs, we logged multiple visits in a night whenever a photo or cluster of photos was separated by an interval of $\geq$20 min. We did not apply the 20-min restriction if a visitor's features unequivocally identified it as different from the previous animal (e.g., a juv and an ad or animals with markedly different white chest blazes). We also noted the number of photos taken per individual. When we determined visitation by spoor in sand pads, we recorded only one visit for the night. We defined visits confirmed by animal photographs as definite and those by sand pad evidence as probable.

Statistical Analysis

We used Microsoft Excel 2004 for Macintosh version 11.0 (Microsoft, Redmond, WA) to perform a series of chi-square contingency analyses, assigning significance at $P \leq 0.05$. For the captive study, our contingency analyses examined the effect of a variety of independent variables on the rates at which animals uncovered surface-level bait, excavated baited and unbaited mounds, and removed surface-level and buried bait. To determine whether there was an effect from mound construction per se, we also performed a contingency analysis using presence of bait within a mound as the independent variable and mound excavation as the dependent variable.

For the field study, our contingency analyses examined the effect of bait burial method on the rates at which devils visited stations, baited and unbaited holes or mounds were excavated, and bait was removed. We conducted these analyses for each phase (western and eastern sections of the park) individually, and for the study as a whole. Because 2 of the 16 observation stations in the western section were never visited by any species, we also performed a separate set of analyses excluding those stations.

To get a better idea of removal rates, we performed an additional set of contingency analyses on data for only those observation station–nights when devil visitation occurred. We analyzed this data set twice, once including and once excluding probable devil visitation (suggested by spoor evidence but unconfirmed by photographic evidence because of occasional camera malfunction). To determine whether there was an effect from hole digging or mound construction per se, we also performed contingency analyses using bait presence within a hole or mound as the independent variable and visitation and excavation as the dependent variables.

RESULTS

Captive Study

Given the few animals involved in the captive study ($n = 11$), we decided to offer baits to the same animals on multiple occasions. Accordingly, the results we describe in this section are not based on truly independent data; that is, each animal contributed to 9 of the 99 data points used in each contingency analysis. As such, these results should not be considered for strict hypothesis testing. Nevertheless, the data reported are useful for exploratory purposes to help discover behavioral patterns that may apply in wild devil populations.

There was no difference in excavation rates between baited and unbaited mounds ($\chi_1^2 = 1.3$, $P = 0.254$), suggesting that presence of a mound was in itself of interest to captive devils. Devils removed surface-level bait 4.4 times more often than bait buried beneath a sand mound ($\chi_1^2 = 42.8$, $P \leq 0.001$). When we compared the 3 mound heights (15 cm, 20 cm, and 25 cm), we found no difference in rates of excavation of baited mounds ($\chi_2^2 = 0.6$, $P = 0.729$), excavation of unbaited mounds ($\chi_2^2 = 0.2$, $P = 0.912$), or removal of buried bait ($\chi_2^2 = 3.2$, $P = 0.199$). In other words, animals were equally likely to excavate mounds of all 3 heights, and mound height had no bearing on removal of bait from excavated mounds.

Captive devils showed a wide range of preference for Foxoff bait. Animals generally uncovered surface-level baits but did not necessarily remove them. Of the 9 surface-level baits placed in each enclosure, devils uncovered a mean of 7.9 (range = 4–9, SD = 1.83) but removed a mean of only 5.4 (range = 0–9, SD = 3.22). Number of days we used a bait did not affect animals' uncovering of surface-level bait ($\chi_4^2 = 6.4$, $P = 0.174$), removal of surface-level bait

($\chi_4^2 = 7.6$, $P = 0.107$), or removal of buried bait ($\chi_5^2 = 6.4$, $P = 0.268$). However, animals were generally more likely to excavate mounds with newer bait than older bait ($\chi_5^2 = 15.8$, $P = 0.007$): they excavated 32 of 47 (68%) new baits; 12 of 29 (41%) 1-day-old baits; 3 of 11 (27%) 2-day-old baits; 1 of 7 (14%) 3-day-old baits; 0 of 3 (0%) 4-day-old baits, and 1 of 2 (50%) 5-day-old baits.

Male animals were more likely than females to exhibit all 5 measured behaviors: males uncovered surface-level bait 1.3 times more often ($\chi_\Delta^\Theta = \Phi.6$, $P = 0.004$), removed surface-level bait 2.4 times more often ($\chi_\Delta^\Theta = \Theta\Sigma.\Psi$, $P \leq 0.001$), excavated bait buried beneath a sand mound 1.7 times more often ($\chi_\Delta^\Theta = \Sigma.\Upsilon$, $P = 0.010$), removed buried bait 2.8 times more often ($\chi_\Delta^\Theta = \Xi.\Delta$, $P = 0.043$), and excavated unbaited sand mounds 1.5 times more often ($\chi_\Delta^\Theta = \Pi.\Gamma$, $P = 0.026$). The 2-year-old, captive-born animals were more likely than 4-year-old, wild-caught animals to exhibit 3 of the 5 measured behaviors: younger animals uncovered surface-level baits 1.4 times more often ($\chi_\Delta^\Theta = \Delta\Phi.\Gamma$, $P \leq 0.001$), removed surface-level baits 2.6 times more often ($\chi_\Delta^\Theta = \Theta\Lambda.\Upsilon$, $P \leq 0.001$), and excavated baits buried beneath a sand mound 1.8 times more often ($\chi_\Delta^\Theta = \Sigma.\Xi$, $P = 0.011$). There were no differences in the 2 cohorts' removal of buried baits ($\chi_\Delta^\Theta = \Lambda.\Gamma$, $P = 0.082$) or in their excavation of unbaited sand mounds ($\chi_\Delta^\Theta = \Delta.\Xi$, $P = 0.235$).

The amount of food an animal had received the previous day (none, 250 g, 500 g, or 800 g) did not influence the degree to which animals uncovered surface-level bait ($\chi_3^2 = 2.5$, $P = 0.468$) or removed either surface-level bait ($\chi_3^2 = 3.7$, $P = 0.298$) or buried bait ($\chi_3^2 = 2.2$, $P = 0.535$). There were differences in the degree of excavation of mounds, both baited ($\chi_3^2 = 13.5$, $P = 0.004$) and unbaited ($\chi_3^2 = 13.2$, $P = 0.004$), among the 4 diet treatments. Despite these differences, there was not a consistent pattern along the dietary gradient. Animals that received 800 g excavated 70% of buried baits and 80% of unbaited mounds; those that received 500 g excavated 52% of buried baits and 61% of unbaited mounds; those that received 250 g excavated 0% of buried baits and 9% of unbaited mounds; and those that received no food excavated 63% of both buried baits and unbaited mounds. Given those inconsistent results, we suspect this contingency analysis fell into the 5% of tests that can be expected to have a Type I error.

Field Study

The data on which we based these results may not be wholly independent. Because Tasmanian devils have broad home ranges (Jones 2008), it is likely that some visitation and bait-removal data involved multiple data points from some animals. Nevertheless, because the field study simulated baiting practices used in the Tasmanian government's fox eradication program, we believe the results we report are indicative of devil behavior in response to field conditions.

Cameras recorded a variety of native and introduced animal species visiting the observation stations. Tasmanian devils were overwhelmingly the most frequent visitors (425 visits), followed by wombats (73 visits) and spotted-tailed quolls (32 visits). Less frequent visitors included the brushtail possum (*Trichosurus vulpecula*; 13 visits), short-beaked echidna (*Tachyglossus aculeatus*; 5 visits), Tasmanian pademelon (4 visits), feral cat (2 visits, apparently by the same animal), black rat (1 visit), and possibly eastern quoll (1 visit; photograph suggested the species but was not conclusive).

Several photographs captured devils, spotted-tailed quolls, and brush-tailed possums investigating sensors and cameras, suggesting a curiosity about the apparatus. The flash and sound of the shutter did not seem to deter devils from investigating either baited or control treatments. Many devils were photographed multiple times (range = 1–39 photographs; $\bar{x} = 4.13$, SD = 5.41) during visits that sometimes lasted several minutes. More photographs were taken per visitor at baited treatments (range = 1–39; $\bar{x} = 5.18$, SD = 6.24) than at control treatments (range = 1–14; $\bar{x} = 1.98$, SD = 1.68).

Based on combined results of both phases, devils visited baited mounds 1.7 times more often than unbaited mounds ($\chi_1^2 = 10.4$, $P \leq 0.001$) and visited baited holes 1.3 times more often than unbaited holes ($\chi_1^2 = 10.7$, $P \leq 0.001$). When we considered the phases separately, however, contrasting results emerged. In the eastern section of the park, devils were 2.2 times more likely to visit baited mounds than unbaited ones ($\chi_1^2 = 9.0$, $P = 0.003$), but there was no difference between visitation of baited and unbaited holes ($\chi_1^2 = 1.4$, $P = 0.230$). In the western section, the reverse was true: devils were 2.2 times more likely to visit baited holes than unbaited ones ($\chi_1^2 = 11.9$, $P \leq 0.001$), but there was no difference between visitation of baited and unbaited mounds ($\chi_1^2 = 2.4$, $P = 0.122$). These results may indicate a Type I error in the contingency analysis for one of the sections.

Mound excavation results were consistent with those in the captive study: there was no difference in excavation rates for baited and unbaited mounds ($\chi_1^2 = 1.1$, $P = 0.284$). In the case of hole excavation, by contrast, devils were 2.6 times more likely to excavate a baited hole than an unbaited one ($\chi_1^2 = 26.5$, $P \leq 0.001$).

Unlike devils in the captive study, wild devils appeared to find Foxoff bait uniformly palatable. In the field study, 100% of baits that were fully excavated were also removed. Several holes and mounds were partly excavated, with the bait remaining buried. But in no case did a bait exposed by excavation remain. It is possible that some baits were fully excavated but left in place by one animal, only to be removed by a subsequent visitor. But when bait was removed at stations where photographic evidence showed visits by multiple animals, photographs suggest in 59% of cases (and clearly show in another 14% of cases) that the first animal to excavate the bait was the one to remove it. In the remaining 27% of cases, a subsequent visitor apparently took the bait; however, photographs in those cases do not indicate whether the earlier visitor(s) uncovered the bait.

The bait burial treatment (mound, 5 cm, 10 cm, or 15 cm) had no effect on observation station visitation ($\chi_3^2 = 4.6$, $P = 0.204$). When we considered the 2 study phases

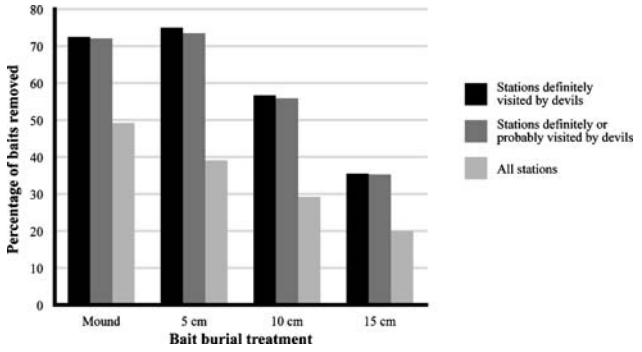

Figure 1. Percentage of buried bait removed by Tasmanian devils under each of 4 bait burial treatments, Narawntapu National Park, Tasmania, Australia, January–February 2008.

separately, burial treatment also had no effect on mound or hole excavation (eastern section $\chi_3^2 = 7.1$, $P = 0.068$; western section $\chi_3^2 = 3.1$, $P = 0.380$). With the greater statistical power achieved by combining the results of the 2 phases, however, burial treatment influenced excavation rates ($\chi_3^2 = 9.3$, $P = 0.025$). Baited mounds were most often excavated (57%), followed by baits buried at 5 cm (42%), 10 cm (35%), and 15 cm (33%).

Finally, burial treatment influenced bait removal ($\chi_3^2 = 14.5$, $P = 0.002$ for both study phases; $\chi_3^2 = 8.5$, $P = 0.037$ for the eastern section alone; $\chi_3^2 = 7.8$, $P = 0.049$ for the western section alone), with overall removal rates decreasing from mounds to 5 cm to 10 cm to 15 cm (Fig. 1).

Because not every observation station was visited by devils on every night, it is more instructive to consider just those data from observation station–nights with known devil visitation (based on photographic evidence) or probable devil visitation (based on spoor in cases of camera malfunction). With data combined from the 2 phases, burial treatment influenced removal ($\chi_{\Lambda}^{\Theta} = \Delta\Xi.\Delta$, $P \leq 0.001$ for definite and probable devil visitation; $\chi_{\Lambda}^{\Theta} = \Delta\Lambda.\Sigma$, $P = 0.004$ for definite visitation only). Removal rates were highest at 5 cm, followed by mounds, 10 cm, and 15 cm (Fig. 1). When we considered the phases separately, burial treatment influenced removal in the western phase ($\chi_{\Lambda}^{\Theta} = \Delta\Gamma.\Lambda$, $P = 0.016$ for definite and probable devil visits; $\chi_{\Lambda}^{\Theta} = \Psi.\Lambda$, $P = 0.026$ for definite visits only) but not in the eastern phase ($\chi_{\Lambda}^{\Theta} = \Xi.\Gamma$, $P = 0.265$ for definite and probable devil visits; $\chi_{\Lambda}^{\Theta} = \Lambda.\Pi$, $P = 0.314$ for definite visits only). We suspect that low statistical power was responsible for the lack of significance for the eastern phase.

DISCUSSION

Bait Removal vs Consumption

We reported bait removal rather than consumption because we cannot be certain how many removed baits were consumed. In their study of Foxoff uptake by spotted-tailed quolls in New South Wales, Körtner et al. (2003) found that animals discarded a high percentage of removed baits. This may be also true for Tasmanian devils. Given the enclosure size in the captive study, we were unlikely to miss baits that had been removed but discarded elsewhere on the surface. However, we could not determine whether devils had cached or discarded baits in their dens. In the field study, we searched the immediate area for discarded baits but could not rule out bait caching or more distant discarding.

The apparent difference in bait palatability between captive and wild devils may be attributable to dietary circumstances. Captive animals that have learned to expect regular feeding by humans may be more likely to ignore or reject slightly unpalatable food than would wild animals accustomed to periods of deprivation. It is also possible that toxic bait would be less palatable than non-toxic. Although 1080 is odorless and tasteless to humans, a study in Western Australia suggested that the fat-tailed dunnart (*Sminthopsis crassicaudata*), a small dasyurid, found 1080-laced bait less palatable than a non-toxic version of the same bait (Sinclair and Bird 1984). Körtner and colleagues (2003) speculate that the same may be true of spotted-tailed quolls.

Our captive results suggest that demographic factors may influence devils' responses to buried bait. If those results can be generalized to wild devils, a tendency for males to excavate and remove bait more frequently than females would likely lessen the impact of poisoning at the population level for several reasons. First, the number of breeding females in a population is an inherently limiting factor for population growth. In devils, the maximum theoretical number of young in a year is 4 times the number of breeding females, as females can raise only 1 litter per year and each of the 4 mammae can support only 1 young (Jones 2008). Second, males are larger than equivalently aged females (Owen and Pemberton 2005, Jones 2008) and would therefore need to locate and consume more baits in a given period to be at risk. Finally, female devils are solely responsible for the rearing of young (Russell 1984), so the effect of individual female deaths is often amplified: only those juveniles on the verge of independence would have much chance of surviving the mother's death.

Differences between the 2 age–provenance cohorts in the captive study are less conclusive. Even if our results can be generalized to wild populations, we do not know whether the observed effect resulted from differences in age, provenance, or some combination of the two. If the pertinent factor is age, younger devils may be more susceptible than older ones to a poisoning program—a cause for concern given the high proportion of young animals in the devil population in DFTD-affected areas (Jones et al. 2008). And because younger animals are smaller, it would take fewer baits to put them at risk.

Baited and unbaited mounds were equally likely to be excavated, whereas baited holes were significantly more likely than unbaited holes to be excavated. This finding suggests that sand mounds may be an intrinsic source of interest to devils but that backfilled holes are not. Devils may be interested in mounds simply as a new feature of their environment worthy of exploration, or they may associate mounds with other animals' food caches or humans' burial of garbage. Whatever the reason, this finding may warrant subterranean over mound burial of baits.

Ultimately, the most important behavior we examined may not be visitation or excavation, but bait removal. That removal rates for the more accessible treatments (mound and 5 cm) were twice those of the least accessible treatment (15 cm) suggests that deeper burial may be warranted—although devils excavated and removed a sizeable percentage even of bait buried at 15 cm.

The scope of our study did not allow us to quantify mortality risk to Tasmanian devils from a fox-baiting program. However, our findings suggest that fox-baiting programs may pose some risk to individual devils. Given that each 35-g Foxoff bait contains 3 mg of 1080, a devil would need to consume only 49 g of Foxoff (1.4 baits) per kg of body mass to receive the median lethal dose of 4.24 g per kg (McIlroy 1981)—an amount well within the devil's capability at one meal (Pemberton and Renouf 1993). Appetite level is therefore unlikely to be a limiting factor in wild devils' consumption of Foxoff baits.

It is important, however, to distinguish between the risks to individuals and populations (Soulé 1985, Choquenot and Ruscoe 1999). The threat that an established fox population would pose to devils and other non-target species may outweigh the individual mortality risk from poisoning. Fox eradication efforts on the mainland usually achieve a net benefit for native species despite a certain amount of non-target species mortality (Glen et al. 2007).

MANAGEMENT IMPLICATIONS

Burying baits at a depth of 5 cm poses a greater risk to devils than would deeper burial. However, the same may well be true of foxes. We could find no published field studies investigating the effect of burial depth on the likelihood of foxes excavating Foxoff or other 1080-laced bait. A high priority for future research is thus a study to determine the degree of bait uptake by foxes under different bait burial treatments. Because fox density is still believed to be very low in Tasmania, such research should to take place on the Australian mainland. Given the high rates of bait uptake by Tasmanian devils even with burial at 15 cm, further research is needed to determine what burial depth would be a more definite deterrent to devils.

Until more reliable data about mortality risk to native carnivores become available, managers should earmark resources for monitoring any effect on native species populations in areas where poisoning occurs. Ongoing capture-mark-recapture studies in areas subject to repeated poisoning campaigns would help to identify any population decline in non-target species. If such monitoring suggests a negative impact on non-target populations, managers should revisit their cost-benefit analysis of the poisoning program.

Our study also confirmed efficacy of using remote cameras to assess Tasmanian devil behavior in response to buried Foxoff baits. Although it would not be practical to deploy remote cameras everywhere poisoning takes place, wildlife managers should consider increasing the use of such equipment at representative baiting sites to determine whether devils and other non-target species are removing bait.

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