Behaviour of an asocial carnivore in a social context:

Social organisation of Tasmanian devils (*Sarcophilus harrisii*)

at the individual level

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A thesis submitted in partial fulfilment of the requirements for the degree of Master of Research.

To the examiners,

This thesis is written in the form of a journal article from Animal Behaviour. Where Macquarie University formatting requirements differed from those of the journal, the university guidelines were followed.

Declaration

I wish to acknowledge the following assistance in the research detailed in this report: Jennifer Clarke for assistance with research design, administrative work and behavioural analysis, and Christopher Davis for assistance with the progam used for calculating dominance scores. All other research described in this report is my own original work.

Kelly L. Davis

9 October 2014

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Running title: Social organisation of Tasmanian devils at the individual level

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Word count: 7919

Submitted 9 October 2014.

ABSTRACT

The Tasmanian devil (*Sarcophilus harrisii*) is currently listed as endangered due to Devil Facial Tumour Disease (DFTD). Attempts to save this species from extinction include the establishment of a captive insurance population, with many individuals housed in managed environmental enclosures (MEEs). These enclosures are intended to closely resemble natural conditions for the devil, and aim to preserve natural behaviours within the captive population.

To investigate if stable dominance hierarchies exist among devils in MEEs, 70 group-feeding events were audio-video recorded across six reproductive enclosures at Devil Ark (Barrington Tops, NSW) over a 4-month period (April-July 2014). Interactions between a devil approaching food and devils already feeding were analysed according to three possible outcomes: failure, displacement and mutual tolerance. Based on these outcomes, dominance scale scores (BBS method) were calculated for the devils in each enclosure for each month. Results revealed that none of the enclosures exhibited stable dominance hierarchies. However, life history traits of the devils, and time spent feeding did influence contest outcomes, with similar trends having been observed in wild devil populations. The results presented here, when compared with wild observations, reflect positively on the captive environment at Devil Ark both in recreating wild conditions and conserving natural behaviours.

Keywords: Dominance hierarchy, group feeding, Dasyurid, captive breeding program, conservation.

1. INTRODUCTION

Dominance has been defined as repeated agonistic encounters between two individuals, in which one consistently wins (termed 'dominant') and the other consistently loses (termed 'subordinate') and the loser will yield rather than escalate the encounter (Drews 1993). Outcomes of these agonistic interactions are subject to the resource holding potential (RHP) of each individual, which is often correlated with age, size and/previous fighting experience and outcomes (Rowell 1974; Kaufmann 1983), the inherent aggressiveness of each individual, and their motivation (subjective resource value) (Hurd 2006).

During these agonistic encounters, each individual must compare the cost of yielding with the cost of persisting (Kaufmann 1983). The establishment of dominance hierarchies functions to regulate resource allocation (de Luca & Ginsberg 2001) with dominant individuals typically have immediate priority of access to resources (Kaufmann 1983). These resources, such as territories, food and access to mates ultimately result in increased fitness. Thus, the cost of yielding is to lose access to these resources and their associated fitness benefits. The costs of persisting however, include time, energy and potential injury (Kaufmann 1983).

Dominance hierarchies are common in species that live in stable social systems, such as canids (e.g. coyotes, *Canis latrans*, Gese et al. 1996; and gray wolves, *Canis lupus*, Sands & Creel 2004), primates (Rowell 1974), mongooses (e.g. banded mongooses, *Mungos mungo*, de Luca & Ginsberg 2001; and meerkats, *Suricata suricatta*, Clutton-Brock et al. 2001). However, solitary species have also been observed to establish dominance hierarchies when competing for certain resources or when a resource (in particular food resources) is unevenly distributed (e.g raccoons, *Procyon lotor*, Gehrt & Fritzell 1998; griffon vulture, *Gyps fulvus*, Bosè & Sarrazin 2007; and boto, *Inia geoffrensis*, de Sá Alves et al. 2013). The establishment of dominance hierarchies in these feeding contexts minimises the risk of injury that would result from escalated agonistic encounters.

The presence of dominance hierarchies in Tasmanian devil (*Sarcophilus harrisii*) assemblages has been debated in the literature, as devils are typically solitary but do associate with one another during feeding, mating, and when females interact with their

offspring (Buchman & Guiler 1977; Pemberton & Renouf 1993; Jones 1995; Hamede et al. 2008). Devils, however, are a timid and nocturnal species and therefore, much of their natural behaviour remains unknown (Buchman & Guiler 1977). The first recorded observations of dominance in devils focused on captive individuals housed in pairs (Buchman & Guiler 1977). It was noted that agonistic interactions occurred frequently upon first introduction and progressively declined as the dominant-subordinate relationship became established. The frequency of these interactions appeared to be influenced by the behaviour of the subordinate individual through increased avoidance of the dominant devil (Buchman & Guiler 1977). Although their observations regarding dominance were restricted to interactions between dyads in captivity, Buchman and Guiler (1977) postulated that wild devils that come into contact regularly, during communal feeding on large carcasses, may form 'truce relationships'. They further proposed that these cooperative groups attack and exclude unfamiliar conspecifics. This suggests that wild devils may establish dominance relationships, and are able to discriminate between individuals, at the very least recognising familiar and unfamiliar devils.

Pemberton and Renouf (1993), however, refuted the hypothesis made by Buchman and Guiler (1977) regarding 'truce relationships' within feeding groups. Based on observations of group feeds in wild devil populations, they concluded that, in devils, dominance is held by the individual that is feeding and, once that individual is satiated, the (previously subordinate) approaching devil becomes dominant. This observation aligns with a 'priority of access to resources' definition of dominance (Drews 1993) which has been observed in other carnivores (eg. spotted hyaenas, *Crocuta crocuta*, Tilson & Hamilton III 1984; and coyotes, *C. latrans*, Gese et al. 1996). However, both coyotes and hyaenas are highly social, pack species, unlike the solitary devil. Additionally, Pemberton and Renouf (1993) did not interpret their observations as evidence of a pecking order dominance structure, instead aligning more to a model where the most motivated (i.e. hungry) individuals win encounters. Although refuting Buchman and Guiler's (1977) hypothesis regarding dominance in devils, Pemberton and Renouf (1993) did concede that dominance was not a focus of their study. They also acknowledged that in order to confirm the existence of dominance hierarchies, repeated observations of known individuals were required, and this information was lacking from their study.

Jones (1995) expanded on the work by Pemberton and Renouf (1993) to investigate devil feeding activity. The interactions between devils, where an individual (initiator) approaches another feeding devil (possessor), were examined, with three possible outcomes identified: failure to gain access; displacement of the possessor; and mutual tolerance (Jones 1995). Jones (1995) stated that sub-adults were more likely to displace each other and adult males than share the carcass; however, they rarely displaced adult females. Adult males allowed females and sub-adults access to the carcass despite being larger and therefore more likely to win contests. Jones (1995) suggested that sub-adults rarely share, and are more likely to displace devils due to their dominance relationships being in a state of flux. The numerous reports of mutual tolerance contradict the observations by Pemberton and Renouf (1993), that devils typically yield when satiated, rather than feed simultaneously. Instead, Jones (1995) observed that the likelihood of mutual tolerance increases as devils become satiated. This work provides a baseline of devil feeding behaviour in wild populations, although Jones (1995) acknowledged that investigations into the social organisation of devils at an individual level were required.

Research into biting rates in devils has revealed that adults have the highest rate of injury and that these injuries occur predominately in the breeding season (Hamede et al. 2008). This trend is expected as devils are a polygamous species, with males fighting one another for access to females, and guarding them in dens post-copulation (Owen & Pemberton 2005). However, as feeding events would also be expected to have high levels of competition and therefore aggression, it is reasonable to assume that there is some mechanism by which aggression levels are kept at a minimum. Jones (1995) suggested that competition is translated as an increase in feeding rate rather than abandoning feeding to engage in agonistic encounters. However, the establishment of dominance hierarchies in groups of familiar conspecifics may also explain the lower aggression during feeding, with subordinate devils yielding instead of escalating interactions, allowing both individuals to avoid costly injury.

Currently listed as endangered (Hawkins et al. 2008), the Tasmanian devil's numbers continue to drop due to the contagious cancer, DFTD. In an attempt to save this species from extinction, an insurance population has been established in Tasmania and on mainland Australia. Captive breeding programs often play a major role in conservation efforts, building up species numbers in a secure and controlled

environment (Eisenberg & Kleiman 1977; Frankham et al. 2010). Unfortunately, many of the early programs ultimately failed due to the inability of captive-bred individuals to properly develop the behaviours necessary for survival in the wild (Kleiman 1989; Grey-Ross et al. 2009). In particular, the inability to recognise and respond appropriately to predators and/or prey have had huge impacts on rehabilitation success (Heezik et al. 1999; Alonso et al. 2011). Effective communication with conspecifics is also critical for survival, from attracting a mate, to understanding warnings such as alarm calls and threat displays (Beani & Dessí-Fulgheri 1998; Liu et al. 2014; Slade et al. 2014). With this in mind, managed environmental enclosures (MEEs) have been developed to house the majority of the captive devil population. These enclosures are much larger (2-5ha) than typical intensive zoo enclosures and hold a larger number of devils (6-8). Tasmanian devil MEEs provide a unique opportunity to study the behaviour of this shy and elusive species in semi-natural conditions. Having multiple devils able to move freely within a large but enclosed space allows social interactions between devils, in particular, group feeding events that are more representative of wild contexts, to be observed, while still allowing controlled sampling.

It has been observed that dominance hierarchies may develop in captive groups of animals but not in their wild counterparts (Richards 1974; Rowell 1974; Kaufmann 1983). Evidence suggests that this is the result of issues with the captive environments, such as overcrowding, unnatural group composition, stressful stimuli, insufficient means of escape for the weaker individuals, and unnatural food distribution (Rowell 1974; McCarthy et al. 1999; Thomas et al. 2003; Mueller 2008; de Sá Alves et al. 2013). As such, examining behaviours related to dominance interactions in captive populations may be a means of evaluating and monitoring animal welfare in these environments. Appropriate captive conditions are important for reproductive success (Taylor & Poole 1998; Carlstead et al. 1999) and to ensure that natural behaviours are maintained (Eisenberg & Kleiman 1977; McPhee 2004; Frankham et al. 2010).

The goals of this study were to assess the social organisation of captive devils during group feeding events at the individual level, by testing the following hypotheses: H1: Tasmanian devils housed in managed environmental enclosures exhibit stable dominance hierarchies during group feeding events.

P1: Dominance ranks calculated based on contest outcomes between known individuals will be consistent across multiple observation periods, based on observations of captive devils by Buchman and Guiler (1977).

H2: Life history traits of Tasmanian devils housed in managed environmental enclosures will influence contest outcomes.

P1: Older individuals will be less successful in contests than younger individuals, based on observations by Jones (1995).

P2: Females will be more successful in contests than males, based on observations by Jones (1995).

P3: Females with pouch young will be more successful in contests than females without pouch young, based on observations of aggression levels by Hamede et al. (2008).

P4: Wild-caught individuals will be less successful in contests than captive raised individuals.

H3: Time already spent feeding during a group feed will influence contest outcome

P1: Time spent feeding is positively related to success in contests during feeding, based on observations by Jones (1995).

Analysis of these aspects of the social organisation of devils in MEEs, with comparisons to observations made of wild individuals, will allow for a greater understanding of how natural devil behaviours are conserved in the captive environment. With ultimate goals of releasing the insurance population back into the wild, maintaining these behaviours is crutial for the future suvival of this species.

2. METHODS

2.1 *Study locations and animals*

This study was conducted on captive Tasmanian devils housed in six managed environmental enclosures (MEEs; Figure 1) at Devil Ark (Barrington Tops, NSW - 31.821767, 151.465486) from April-July, 2014. All enclosures conformed to husbandry guidelines for Tasmanian devils (Hogg & Hockley (eds). 2013). Enclosures housed four to 12 individuals and were 2-4 ha with a fence height of 1.8 m. All enclosures included den structures, vegetation, logs, rocks and trees. Individuals had *ad libitum* access to water and were fed raw meat (e.g. kangaroo, poultry, rabbit) once daily, with the exception of scheduled starve days. A total of 40 Tasmanian devils, in six, mixed sex reproductive MEEs were used in this study (Table 1).

Table 1. Summary of the devils in each enclosure recorded during this study at Devil Ark, Barrington Tops, NSW. Devil IDs represent the studbook number for each individual, their sex (F=female, M=male), and their age in years at the time of this study. During the recordings made in May, June and July, enclosures F6 and F8 were joined.

	Enclosures					
	F3	**F5**	**F6**	**F7**	**F8**	**F9**
	1142F3	1314F2	1148M3	1132F3*	1045F4	1035F4
	1295F2	1147F3	1197F2	969F4	1189F2	1290F2
	1178F3	1226F3	1288F2†	1307F2	1151F3*	1096F3
Devil	934F4	1187M2	1026F4	936M4	930M4	1116F3
IDs	962M4‡	1068M4	961M4	823M5 ψ	892M5	1067M4
	1181M3‡	900M5	899M5	1149M3	815M5	933M4
	1044M4				967M4	1146M3
						975M4

* = Females moved to intensive enclosures after April recordings
† = Female moved to F7 for May and June recordings
ψ = Male moved to F6/8 for May and June recordings and removed for July recordings
‡ = Males moved out of F3 for the July recordings

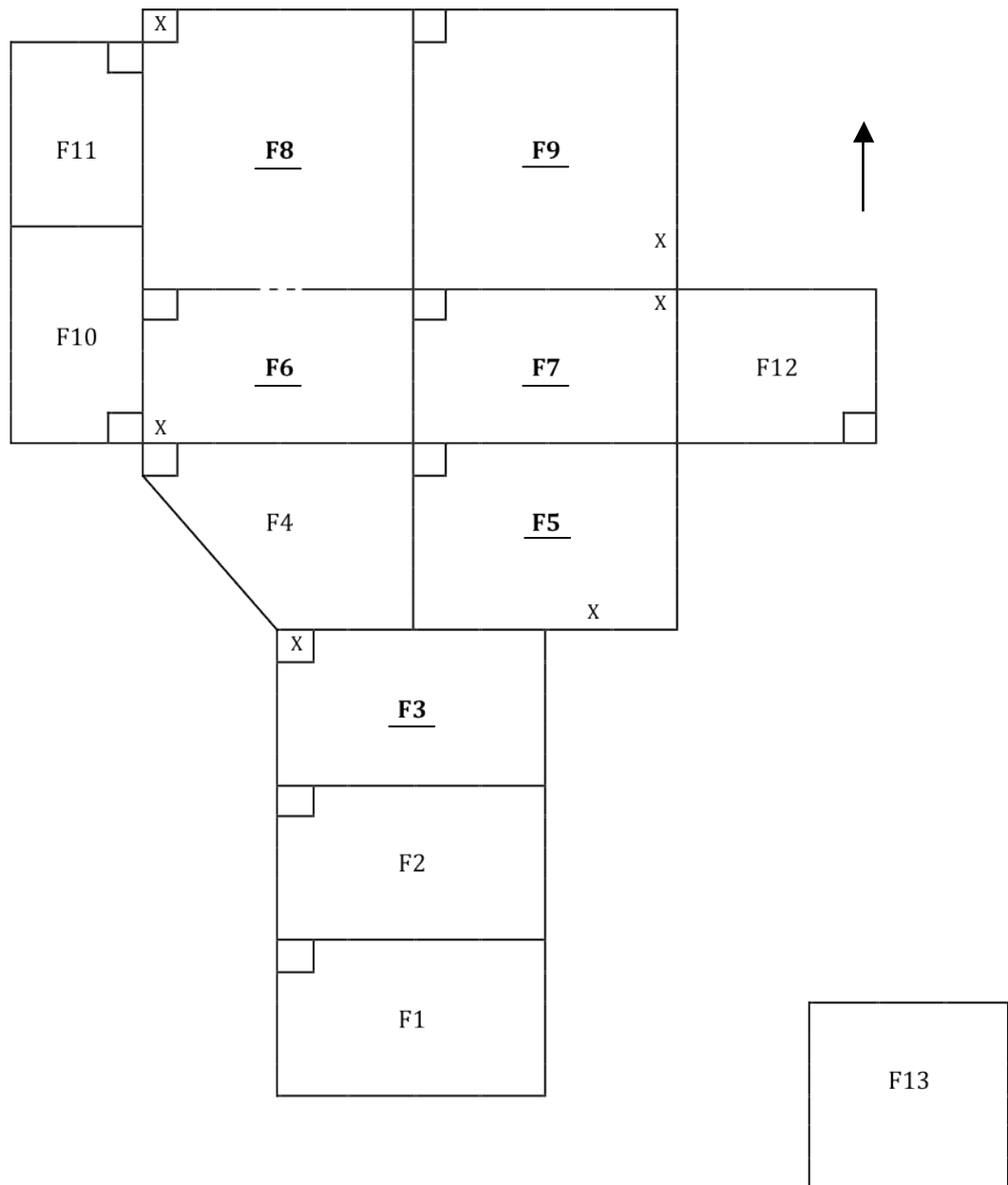**Figure 1.** Diagram of the Tasmanian devil managed environmental enclosures (MEEs) at Devil Ark, Barrington Tops, NSW. Enclosures in bold/underlined indicate reproductive enclosures that were used in this study and 'X's indicate the locations of the feeding stations. The smaller boxes represent 'air-locks' and the broken line between enclosures F6 and F8 indicate where the enclosures were joined after the April recordings.

2.2 *Ethical considerations*

This study was conducted in accordance with the Australian Code of Practice for the Care and Use of Animals for Scientific Purposes (NHMRC, 1997). This research was approved by the Save the Tasmanian Devil Program Captive Research Advisory Group (12/02/2014, Hogg, C; Appendix 1), and the Macquarie University Animal Ethics Committee (protocol number 2013/037; Appendix 2).

2.3 *Data collection*

2.3.1 *Video recording*

Devils housed in MEEs were recorded during feeding, using video recorders (Sony Handycam DCR-HC36, Sony Handycam DCR-HC38, Sony Handycam HDR-PJ760; Sony, Minato, Japan). Recordings of group feeding events involved a Devil Ark keeper attaching food (kangaroo meat) to a stake in the ground (to prevent it being removed by the devils) and allowing the devils to congregate at these feeding stations (Figure 1). Cameras were set up outside the enclosures and left to record remotely for at least 60 min (between 14:00 and 18:00), to minimise the influence of human presence on the devils' behaviour. Each enclosure was recorded for three consecutive feeds over 1 week every month for 4 months (April-July). Enclosures were always recorded in the same order and never on a Saturday, as this was the scheduled starve day for all enclosures (Table 2). Enclosures F6 and F8 were joined during the May-July recordings, however, two feeding stations were still set up in this joint enclosure at the same locations used for the April recordings (Figure 1).

Table 2. Schedule for the group feeding events recorded at Devil Ark, Barrington Tops, NSW, April-July 2014.

	Day					
	Sunday	**Monday**	**Tuesday**	**Wednesday**	**Thursday**	**Friday**
Enclosures recorded	F5	F5	F5	F3	F3	F3
	F7	F7	F7	F6	F6	F6
	F9	F9	F9	F8	F8	F8

2.3.2 *Video scoring*

Video files of group feeding events were imported into iMovie (version 8.0.6) and then exported as .mp4 or .mov files to be reviewed in Quicktime Player (version 7.6.6) on a Macintosh OS X (version 10.6.8). Approaching events, where an individual approaches the food attached to the feeding stake during the group feeds, were scored. Specifically, the individual approaching, the time of approach, duration of approach, which devil(s) already feeding responded to the approaching individual, the outcome of the approach (failure, mutual tolerance or displacement; Table 3), the time at which each individual left the feed station and the stimulus related to leaving, were recorded. In all cases, the identities of the devils involved in the behaviours were noted.

Table 3. Definitions of the three possible outcomes of approaches by individuals to feeding conspecifics during group feeding events of Tasmanian devils.

Outcome	Definition
Failure	Approaching devil is unsuccessful at gaining access to meat due to the responses of the individual(s) already feeding, described by Jones (1995).
Mutual tolerance	Approaching devil gains access to meat and feeds along side the individual(s) already feeding, described by Jones (1995).
Displacement	Approaching devil gains access to meat by displacing the individual(s) already feeding, described by Jones (1995).

Devils were identified based on their unique white pelage markings and scarring, observed in the videos, and by comparing these with the photo ID sheets created by the Devil Ark keepers for each animal. Additionally, life history information for each individual was recorded, including: age, sex, last recorded weight, reproductive history, sire, dam, and origin (Figure 2).
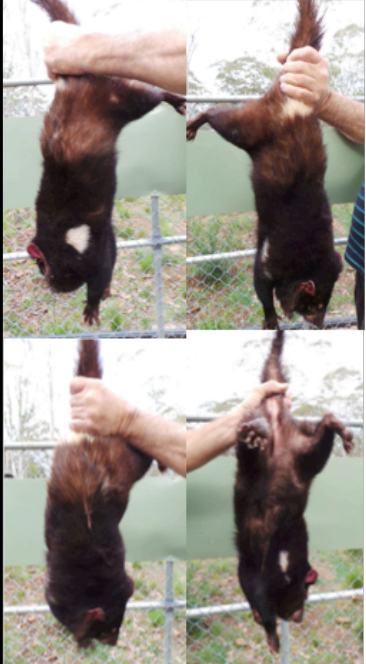
Figure 2. Example of a devil ID sheet, for individual 1226F3 in enclosure F5 at Devil Ark, Barrington Tops, NSW. Photos on the left were taken by Devil Ark keepers during routine external examination (grasping devils by the tail is an approved handling method, minimising risk to both devil and handler) and the photos on the right are screen shots from the video footage.

2.4 *Data analysis*

2.4.1 *Contest outcomes*

For each approaching event, a 'win' was assigned to an individual if they displaced a feeding devil as they approached the food, or if, while feeding, they responded to an approaching devil, resulting in that devil failing to access meat (aborting their approach). Conversely, a devil was considered as having 'lost' when they failed to access the food (aborted their approach) due to the response of a feeding devil, or they were displaced by an approaching individual while they were feeding. If a devil aborted their approach but there was no detectable response from any devils already feeding, this event was discarded. For all instances where an approach resulted in mutual tolerance, all individuals feeding were scored a tie with the approaching individual.

2.4.2 *Dominance hierarchies*

2.4.2.1 *Calculating dominance rank*

      For each enclosure, a t x t matrix of dominance interactions (hereafter dominance matrix) was created based on the outcomes of the approaches by each devil (described above). To determine whether the dominance structure remained stable over time (April – July), a separate dominance matrix was made for the observations of each enclosure for each month, resulting in four matrices per enclosure. In order to factor in ties (approaches resulting in 'mutual tolerance') a symmetric matrix describing the total number of interactions between each dyad was created for each set of observations for each enclosure. Based on these matrices, the dominance scale scores for each individual were calculated using the BBS (Batchelder-Bershad-Simpson) method, described by Jameson et al. (1999), that was modified to allow for ties. Initial scale scores (s(a_i)) were calculated for each individual using the formula:

$$s(a_i) = [\alpha(2W_i + T_i - N_i)/2N_i]$$

where $\alpha = \sqrt{2\pi} = 2.50663$ is a constant (Jameson et al. 1999), W_i is the number of encounters that a_i was observed having won, T_i is the number of encounters involving a_i that resulted in a tie, and N_i is the total number of encounters in which a_i was involved.

The scale scores obtained from this initial equation were then used in a second formula, which was used recursively until the scores (s(a_i)) for each individual converged, or for a maximum 50 iterations:

$$s(a_i) = [2(W_i - L_i)/N_i] + Q_i$$

where L_i is the number of encounters that a_i was observed having lost, and Q_i is the mean scale scores from the previous iteration for all the individuals that a_i encountered.

2.4.2.2 *Testing for stable dominance hierarchies*

      When scale scores had been calculated for each individual for each of the four observation months, Kendall's coefficient of concordance (hereafter Kendall's W) was used (exact test) to determine whether the dominance scores within each group of devils were stable across the entire observation period. Since there was some movement of devils between enclosures (Table 1), Kendall's W tests were conducted on

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the scores of the individuals present for all the observation months as well as the scores for all individuals present for three of the four observations months. For the F6/8 enclosure, Kendall's W was run on the scores of all individuals present for all 3 months after the enclosures had been merged, as well as on the scores of the individuals present in the April recordings in F6 and F8 for the four observation months, separately. All statistical analysis was conducted using SPSS (IMB SPSS Statistics, version 21).

2.4.3 *Influence of life history traits on contest outcome*

2.4.3.1 *Data collection*

Based on the life history information provided by the Devil Ark keepers, age, sex and reproductive status were determined for all individuals. To investigate the influence of age on contest outcome, the age of the approacher, relative to that of the feeder (older, same, younger), was determined for all of the observed interactions (N=2185). Information regarding the reproductive status of the females included in this study was provided by the Devil Ark keepers following routine pouch checks (September, 2014). Based on the development of the joeys, the oestrus cycle during which females reproduced successfully was established (Guiler 1970a; Phillips & Jackson 2003). This information was used to determine during which observation months the females were carrying pouch young (first oestrus: April-July recordings, second oestrus: May-July recordings, third oestrus: June-July recordings). The reproductive statuses of individuals were then categorised into one of three groups: females with pouch young, females without pouch young, and males.

2.4.3.2 *Statistical Analysis*

A Pearson's Chi-squared (exact) test was used to test for an association between the age of the approacher (older, same or younger) and the outcome of the interaction (displacement, failure or mutual tolerance). Cross tabulation of the two variables was also conducted, with standardised residuals, to determine which specific interactions differed significantly from the expected results.

The effects of sex and reproductive status on contest outcome were both analysed using three-way log-linear analyses. Cross tabulation of sex and reproductive status of approachers and interaction outcomes with feeders as the first layer were also conducted, with standardised residuals, to determine which specific interactions differed significantly from the expected results.

2.4.4 *Influence of feeding time on contest outcome*

2.4.4.1 *Data collection*

Based on the approach times, approach durations and time leaving for each individual, the time already spent feeding by the approaching devil and feeding devil at the time of approach was calculated for each interaction. These were grouped into three categories (<15 min, 15-30 min, >30 min). However, as there were so few interactions where the approaching individual had already fed for >30 min, these interactions were removed from further statistical analysis.

2.4.4.2 *Statistical analysis*

The effect of time already spent feeding for both the approaching individual and the feeding individual on the outcome of the interaction was analysed using a three-way log-linear analysis. Cross tabulation of feeding time of the approacher and outcome, with feeding time of feeder as the first layer was also conducted, with standardised residuals, to determine which specific interactions differed significantly from the expected results.

3. RESULTS

3.1 *Dominance scale scores*

The dominance scale scores for each individual for the four observation months, demonstrated the fluctuations and consistencies in the rank orders observed in each enclosure (Figure A1a-f). Dominance ranks were not stable across the 4 months for any of the enclosures (Kendall's W range 0.025-0.200, *P* >0.05 all cases; Table 4).

Table 4. Results of the Kendall's W tests to determine whether Tasmanian devils in MEEs at Devil Ark, Barrington Tops, NSW, establish stable dominance hierarchies. The Kendall's W can have a maximum value of 1 (complete consistency) and a minimum of 0 (no consistency). These results therefore indicate that none of the enclosures exhibited stable dominance hierarchies across the 4 months observed.

Enclosure	Months included	N	df	*W*	*P*
F3	April-July	5	3	0.200	0.445
F3	April-June	7	2	0.143	0.486
F5	April-July	5	3	0.040	0.944
F5	May-July	6	2	0.028	0.956
F6	April-July	4	3	0.075	0.900
F6/8	May- July	11	2	0.033	0.732
F8	April- July	4	3	0.025	0.992
F7	April-July	4	3	0.075	0.900
F9	April-July	8	3	0.075	0.654

3.2 *Life history traits and contest outcome*

3.2.1 *Age of individuals*

The age of the approacher relative to the receiver was strongly associated with the outcome of the interaction (Pearson's χ^2_4 = 20.194, *P* <0.001). Older individuals failed significantly more than expected and approachers who were the same age as the feeding individual failed significantly less than expected (standardised residuals of cross-tabulation; *P* <0.05, both cases). Younger individuals displaced older individuals

significantly more than expected (standardised residuals of cross-tabulation; P <0.05; Table 5).

Table 5. The effects of age of the approaching devil, relative to the feeder, on the outcome of the interactions observed during group feeding events in MEEs at Devil Ark, Barrington Tops, NSW. Data are standardised residuals from cross-tabulation of age and interaction outcome. Residuals greater than ±1.96 indicate a significant effect, with the sign of the residual indicating the direction of the effect. N = number of interactions, D = approacher displaced feeder, F = approacher failed to gain access to food, MT = approacher fed with feeder (mutual tolerance).

Age of approacher relative to that of the feeder	N	Outcome		
		D	F	MT
Older	836	-1.4	2.3*	-0.6
Same	563	-0.9	-2.2*	1.3
Younger	786	2.2*	-0.5	-0.4

* P <0.05

3.2.2 *Sex of individuals*

The three-way log-linear analysis revealed that the highest-order interaction (sex of approacher x sex of feeder x outcome) significantly contributed to the model (χ^2_2 = 13.730, P <0.001) and the likelihood ratio of this model was χ^2_0 = 0, P = 1. For female feeders, there was a significant association between sex of approacher and outcome (Pearson's χ^2_2 = 29.155, P <0.001, and the same was true for male feeders (Pearson's χ^2_2 = 78.296, P <0.001). Females approaching females failed significantly less than expected and males approaching females failed significantly more than expected (standardised residuals of cross-tabulation; P <0.01: both cases). Interactions where females approached males resulted in displacement and failure significantly less than expected (standardised residuals of cross-tabulation; P <0.05, P <0.001, respectively), and resulted in mutual tolerance significantly more than expected (standardised residuals of cross-tabulation; P <0.01). Interactions where males approached other males resulted in displacement and failure significantly more than expected (standardised residuals of cross-tabulation; P <0.01, P <0.001, respectively), and in mutual tolerance significantly less than expected (standardised residuals of cross-tabulation; P <0.01; Table 6).

Table 6. The effects of sex of the approaching and feeding devils on the outcome of the interactions observed during group feeding events in MEEs at Devil Ark, Barrington Tops, NSW. Data are standardised residuals from cross tabulation of the sexes of the individuals and interaction outcome. Residuals greater than ±1.96 indicate a significant effect, with the sign of the residual indicating the direction of the effect. N = number of interactions, D = approacher displaced feeder, F = approacher failed to gain access to food, MT = approacher fed with feeder (mutual tolerance).

Sex of approacher-feeder	N	Outcome of interaction		
		D	F	MT
Female-Female	368	1.3	-3.9**	1.5
Male-Female	685	-0.9	2.9**	-1.1
Female-Male	530	-2.3*	-5.2***	3.0**
Male-Male	599	2.1*	4.9***	-2.9**

P <0.05
** *P* <0.01
*** *P* <0.001

3.2.3 *Reproductive status of females*

The three-way log-linear analysis produced a final model that discarded higher order effects (approacher x feeder x outcome). The likelihood ratio of this model was χ^2_{12} = 10.883, *P* = 0.539. For males as feeders, there was no significant association between reproductive status of approacher and outcome (Pearson's χ^2_2 = 0.245, *P* = 0.885). For female feeders both with and without pouch young however, there was a significant association between reproductive status of approacher and outcome (Pearson's χ^2_2 = 26.048, p < 0.001 and χ^2_2 =17.236, *P* = 0.002, respectively). Females with pouch young approaching females without pouch young failed significantly less than expected (standardised residuals of cross-tabulation; *P* <0.05). Females with pouch young displaced other females with pouch young significantly more than expected (standardised residuals of cross-tabulation; *P* <0.001). Females without pouch young failed against females with pouch young significantly less than expected and males approaching females without pouch young failed significantly more than expected (standardised residuals of cross-tabulation; *P* <0.05: both cases; Table 7).

Table 7. The effects of reproductive status (female with pouch young, female without pouch young, male) of the approaching and feeding devils on the outcome of the interactions observed during group feeding events in MEEs at Devil Ark, Barrington Tops, NSW. Data are standardised residuals from cross tabulation of the reproductive status of the individuals and interaction outcome. Residuals greater than ±1.96 indicate a significant effect, with the sign of the residual indicating the direction of the effect. N = number of interactions, D = approacher displaced feeder, F = approacher failed to gain access to food, MT = approacher fed with feeder (mutual tolerance).

			Outcome of Interaction		
Approacher	**Feeder**	**N**	**D**	**F**	**MT**
Pouch young	No pouch young	128	1.3	-2.5*	0.8
Pouch young	Pouch young	58	3.5***	-1.7	0.1
No pouch young	No pouch young	65	-0.2	-1.6	0.8
No pouch young	Pouch young	117	-1.1	-2.0*	1.2
Male	No pouch young	379	-0.6	2.1*	-0.8
Male	Pouch young	305	-0.9	1.9	-0.7
Pouch young	Male	253	0.1	0.3	-0.1
No pouch young	Male	280	-0.1	-0.3	0.1

*P <0.05
*** P <0.001

3.3 *Feeding time and contest outcome*

The three-way log-linear analysis revealed that the highest-order interaction (feeding time of approacher x feed time of feeder x outcome) significantly contributed to the model (χ^2_3 = 21.41, P <0.001) and the likelihood ratio of this model was χ^2_0 = 0, P = 1. For feeders who had fed for <15 min, there was a significant association between feeding time of approacher and outcome (Pearson's χ^2_2 = 28.355, P <0.001). However, for feeders who had fed for 15-30 min and >30 min, there was no significant association between feeding time of the approacher and outcome (Pearson's χ^2_2 = 5.152, P = 0.076 and χ^2_2 = 0.833, P = 0.659, respectively). Approachers who had already fed for 15-30 min displaced feeders who had already fed for <15 min significantly more than expected (standardised residuals of cross-tabulation; P <0.001; Table 8).

Table 8. The effects of time already spent feeding by the approacher and feeder on the outcome of the interactions observed during group feeding events in MEEs at Devil Ark, Barrington Tops, NSW. Data are standardised residuals from cross-tabulation of feeding time of individuals and interaction outcome. Residuals greater than ±1.96 indicate a significant effect, with the sign of the residual indicating the direction of the effect. N = number of interactions, D = approacher displaced feeder, F = approacher failed to gain access to food, MT = approacher fed with feeder (mutual tolerance).

Feeing time (min)		N	Outcome		
Approacher	Feeder		D	F	MT
<15	<15	1490	-1.1	-0.4	0.4
<15	15-30	286	0.3	1.1	-0.8
<15	>30	45	0.3	0.3	-0.5
15-30	<15	80	4.6***	1.5	-1.8
15-30	15-30	176	-0.4	-1.4	1.0
15-30	>30	49	-0.3	-0.3	0.5

*** P <0.001

Although the effect of feed time on contest outcome appears minimal, analysis of the percentages of all interactions resulting in mutual tolerance, failure and displacement according to the time spent feeding by approachers and feeders are worth noting, as the results differ from those reported by Jones (1995). As time spent feeding increased, the percentage of interactions resulting in failure and displacement also increased, with a decrease in the percentage of interactions resulting in mutual tolerance, for both approachers and feeders (Figure 3).
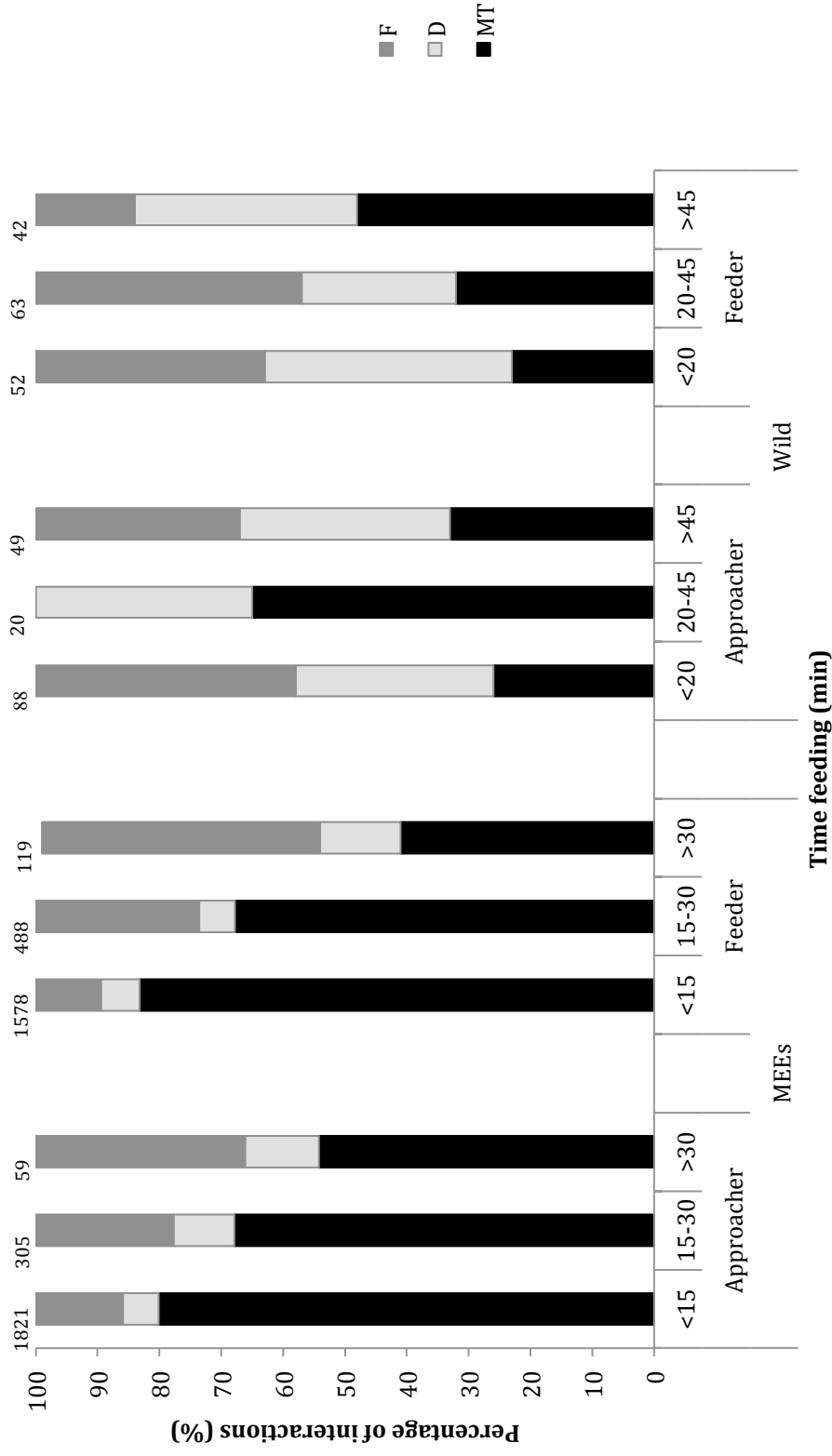
Figure 3. Percentages of all the interactions observed resulting in failure (F), displacement (D) and mutual tolerance (MT) during group feeding events observed at Devil Ark, Barrington Tops, NSW (MEEs) and group feeding events of wild devils with data taken from Jones (1995) (wild). The observations for each population are separated according to the time spent feeding by the approaching devil (approacher) and the feeding devil (feeder). The numbers above each column indicate the number of observed interactions for each category.

4. DISCUSSION

Through extensive observations of interactions of captive Tasmanian devils during group feeding events (40 devils in 70 feeding events with 2185 interactions), this study found no evidence that devils in managed environmental enclosures establish stable dominance hierarchies. However, contest outcome was influenced by identifiable factors, which included static (i.e. sex), fluctuating (i.e. age and reproductive status) and transient (e.g. time feeding) factors. Similar trends have been described by Jones (1995) during observations of group feeding events in wild devil populations. The results presented here also reflect on the success of the MEE environment in replicating wild conditions and conserving the natural social behaviours of devils within the insurance population.

4.1 *Age and contest outcome*

For the devils observed in this study, investigation into the influence of age on contest outcome revealed that younger individuals gained and retained possession of food more than expected but shared with older individuals less than expected. However, interactions between individuals of the same age resulted in displacement and mutual tolerance more than expected and in failure less than expected. Although Jones (1995) combined age and size variables when analysing contests outcomes of wild devils, the results presented here align with her observation that wild sub-adults (younger individuals) fight to retain possession of food against adults (older individuals) and also displace other sub-adults. The differences regarding food sharing between the captive devils in this study and the wild devils in Jones (1995) study may be explained by the differences in population structure. While wild populations will naturally include sub-adults, as the MEEs observed in this study were all reproductive enclosures, they only contained devils of breeding age (2-5 years). It is worth noting that the direction of age bias seen both in MEEs and in the wild is unusual. Typically, priority of access to resources and contest outcomes fall in favour of older (generally correlating with larger) individuals, who have more experience in agonistic encounters (Rowell 1974; Barnard & Burk 1979; Drews 1993; Macdonald et al. 2002; Elfström et al. 2014), with younger individuals exhibiting more tolerance toward one another (e.g. horses, *Equus ferus*, Houpt et al. 1978).

4.2 *Sex and contest outcome*

Trends in contest outcome according to sex were also observed in the MEEs. While Jones (1995) found that females approaching males were equally likely to displace or feed with them, the results of the present study suggest that sharing occurs more than expected when a female approaches a male, and incidences of both displacement and failure were low. The outcomes of interactions where males approach females also differed from Jones' (1995) observations, which described a high likelihood of mutual tolerance, whereas in the present study, males failed more than expected. This study occurred during the devils breeding season. In other species, contest outcome with respect to sex has been shown to be change during the breeding season compared to other times of year (e.g. horses, *E. ferus*, Houpt et al. 1978). As such, investigation into paternity of the females' joeys with respect to how the females respond to approaches by different males in their enclosure may provide further insight into these social interactions. Females approaching each other were found to be just as likely to share as to displace one another in both the wild (Jones 1995) and captive (present study) environment. Although outcomes of interactions between males are not directly discussed for the wild population (Jones 1995), interactions between males in the MEEs resulted in mutual tolerance less than expected and in failure and displacement more than expected.

The lower tolerance between males may be a result of the sex ratios with the MEEs, which differ from natural devil population structures (Guiler 1970b; Pemberton 1990). While the reproductive enclosures at Devil Ark were approximately 1:1, wild devil populations are female biased (2:1) from pouch young through to senescence where females then have a higher mortality rate (Guiler 1970b; Pemberton 1990). Interactions between males may therefore be elevated in the MEE environment. Unnatural male-biased sex ratios have been found to result in elevated aggression levels (e.g. lizards, Alberts 1994; and zebrafish, *Danio rerio*, Spence & Smith 2005), and this has been linked to a decrease in female reproductive success in some lizard species (Alberts 1994). Exploration into contact networks of devils also reflects the trends described here, with 'preferred associations' outside the mating seasons mostly being between females, followed by inter-sexual preferences, with preferred associations between males being relatively rare (Hamede et al. 2009).

4.3 *Reproductive status and contest outcome*

Given the increased aggression by female devils with pouch young towards conspecifics, observed in wild populations (Hamede et al. 2008), the influence of reproductive status on contest outcome was also explored. While interactions between females with and without pouch young mirrored the trends found in the analysis of sex bias in contest outcome, females with pouch young displaced each other more than expected. This may be the result of high motivation for food given the increased energy requirements of nursing young. However, if this were the case, it would be expected that females with pouch young would be less likely to share with all other conspecifics, particularly males, who have higher feeding rates than females (Pemberton & Renouf 1993). In black and brown bears (*Ursus americanus* and *U. arctos*) females with dependent young have higher dominance ranks than solitary females which is thought to be the result of their higher security requirements (Elfström et al. 2014). While devils, being marsupials, are always with their offspring, and therefore share this risk, this again does not explain why the increase in aggression and lack of tolerance appears to be predominantly directed at other females with pouch young. An alternative explanation may be that other females with pouch young represent the future individuals that will be competing with a female's own joeys for resources, and higher aggression towards other females with pouch young may be an attempt to increase one's own reproductive success (Stockley & Bro-Jørgensen 2011).

4.4 *Time spent feeding and contest outcome*

In addition to stable and slowly fluctuating variables influencing contest outcome, more transient factors also had an effect. In cases where the approaching individual had already spent 15-30 min feeding, and the feeder had spent <15 min feeding, the approacher displaced the feeder more than expected. In wild populations, time spent feeding was positively related to incidences of mutual tolerance (Jones 1995). In contrast, the percentage of interactions resulting in mutual tolerance decreased as feeding time increased for both approacher and feeder in the MEEs, and the percentage of interactions resulting in displacement and failure increased.

These inconsistencies in outcome may be the result of a number of differences between the wild and captive group feeding contexts. While the typical carcass size

used for wild observations is ~20kg, food quantities in MEEs are controlled according to the number of devils within each enclosure (~500g per devil) (Pemberton 1990; Pemberton & Renouf 1993; Jones 1995; personal communication with Devil Ark staff). Additionally, a greater number of devils were observed feeding simultaneously in the MEEs (max 9), than observed by Jones (1995) (max 5). Given that devils are able to consume up to 40% of their body weight in a single night, the feeding regime for wild observations created a situation where the food availability exceeded what is required or able to be consumed by the number of devils observed (Pemberton 1990; Jones 1995). As such, competition over food during wild group feeds would have decreased over time as the individuals reached satiation. In MEEs however, the food available to each individual was much more restricted and diminished much faster. For nearly all observed feeds, the food provided was completely consumed or only hard long bones and vertebrae remained at the end of the observation period (60-90 min). Toward the end of the feeds, the number of individuals present decreased, and the remaining food, having been greatly diminished, was more easily defended, potentially more valuable, and more difficult to feed on simultaneously. This likely contributed to the increased displacement and failure rates observed when the devils had been feeding for longer. Observations of group feeds in MEEs where food availability is effectively unrestricted may therefore result in similar trends regarding feed time and contest outcome to those observed by Jones (1995).

4.5 *Number of devils present and contest outcome*

Although not directly examined in this study, there appeared to be some influence of the number of devils present at a feed site and the outcome of approaches, with devils more likely to ignore or tolerate an approaching devil when there were multiple individuals already feeding. Jones (1995) made similar observations and proposed that this behaviour was the response of competition at the food site. While more devils translates to greater competition over a limited food source, devils do not appear to respond with increased aggression or number of agonistic encounters. If a single individual were to respond to the approaching devil, the time spent responding would be deducted from potential feeding time. Additionally, all of the individuals who do not respond would continue to feed, further diminishing the resource. Therefore, the cost of allowing another individual to join the group may be less than the cost of responding and losing feeding time (Jones 1995). If, however, there is only one devil at

the feed site, responding to an approacher may be more beneficial since the resource is not being depleted during the response time and the feeding devil, if successful at driving off the approacher, can maintain sole possession of the carcass. Tolerance is also a beneficial strategy for a devil approaching multiple conspecifics, as displacement of many individuals appears to be more difficult and costly than the displacement of a single feeding devil.

4.6 *Trends in life history traits but no dominance hierarchy*

Dominance hierarchies in devils has often been assumed or alluded to, though not directly tested (Pemberton & Renouf 1993; Jones 1995; Owen & Pemberton 2005; Hamede et al. 2012). This is likely due to the asymmetry in contest outcomes described above and dominant individuals observed in traditional zoo enclosures (Buchman & Guiler 1977). A similar situation has been described for the European badger, *Meles meles* (Macdonald et al. 2002). As a social carnivore, it was assumed that badgers establish linear dominance hierarchies within groups. Like the devils, there were asymmetries in contest outcome between badgers, with body size and food 'ownership' influencing contest outcomes. However, no evidence of dominance relationships were reported. (Macdonald et al. 2002).

For both devils and badgers, the combination of relatively stable and transient variables influencing contest outcomes may explain the lack of stable dominance hierarchies (Macdonald et al. 2002). For example, the outcome of an interaction between the same two individuals varies according to which individual is feeding and which is approaching. For devils, this is particularly evident for sex, as males typically shared the food when approached by females, whereas when a male approaches a female, the male is more likely to fail. The establishment of stable dominance relationships requires repeated encounters with the same individual, and the outcomes of previous encounters to be a good predictor of the outcomes of future interactions (Rowell 1974; Drews 1993). Given the transient nature of some of the variables contributing to contest outcome in devil interactions, the predictive power of past interactions on future contests may be relatively low in this species.

4.7 *The effectiveness of managed environmental enclosures at conserving natural behaviours*

Managed environmental enclosures for breeding Tasmanian devils are a new initiative, developed with an understanding of the importance of maintaining natural behaviours in the captive population in ensuring that future reintroductions of devils into Tasmania are successful (Sinn et al. 2010; DevilArk 2013). In the past, many captive breeding programs have ultimately failed due to captive-born individuals being unable to develop behaviours in the captive environment that are necessary for survival in the wild, including responding appropriately to predators and prey, and engaging in social interactions with conspecifics (Lyles & May 1987; Horwich 1989; Biggins et al. 1999; Alonso et al. 2011). Continued assessment of behaviour in the captive devil population is therefore vital to ensure appropriate management and the program's ultimate success.

Differences in the social interactions between individuals in captive and natural environments have been observed for a range of species, and have been linked to insufficient space, unnatural group composition, overcrowding, stressful stimuli and poor distribution of resources (Rowell 1967; Richards 1974; Kaufmann 1983; McCarthy et al. 1999; Radespiel & Zimmermann 2001). The absence of clear social hierarchies within MEEs may therefore be a positive result for the breeding program. Devils in MEEs are likely to have high numbers of interactions with the same conspecifics. Dominance relationships typically become established from multiple encounters, with previous outcomes often predicting the outcomes of future contests (Rowell 1974; Kaufmann 1983; Drews 1993). The lack of a consistent hierarchy suggests that there is sufficient space and opportunity for weaker individuals to escape and avoid conflict.

Dominance hierarchies have also been documented as a manifestation of the different coping responses of individuals to stress associated with a captive environment (Rowell 1967; Rowell 1974). High stress levels have been reported to impact breeding success in species that have been the target of captive breeding programs (Taylor & Poole 1998; Carlstead et al. 1999). Subordinate individuals may fail to reproduce due to an inability to access sufficient resources, or be unable to raise their offspring to maturity as a consequence of their low position within the group. With this pressure apparently absent in MEEs, the devils should have equal breeding opportunity and output, reducing the chances of genetic adaptation to captivity, and maintaining

natural behaviours in the captive population (McDougall et al. 2006; Frankham et al. 2010).

The trends observed in this study largely align with observations made of wild group feeding events (Jones 1995). Stable (i.e. sex) and fluctuating factors (i.e. age and reproductive status) had an effect on contest outcomes in devils. Younger individuals were generally more successful in contests than older individuals and females were more successful than males. Transient factors, such as time already spent feeding, also influenced contest outcome. While this effect was not consistent with the wild population, the difference in food abundance, number of individuals present and observation time can most likely explain this discrepancy (Jones 1995). Given the overall consistencies between observations of wild devils and the individuals in MEEs, and the absence of stable dominance hierarchies, managed environmental enclosures appear to be effective at recreating wild conditions and conserving natural behaviours of devils with regards to their social interactions during feeding.

ACKNOWLEDGEMENTS

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APPENDICES

Appendix 1 – Approval of research from the Save the Tasmanian Devil Program Captive Research Advisory Group.

Dr Jennifer Clarke
Macquarie University
Sydney
NSW

12th February 2014

Dear Jennifer,

The Captive Research Advisory Group (CRAG) have assessed your request for an extension for the project titled *"Tasmanian devil vocalisations and dominance hierarchies"* until 2017.

The CRAG was impressed by the work that you have achieved on this project to date and approve your extension request without any further conditions.

Please be advised that researchers in Austria who are conducting work on the vocal communication of Tasmanian devils at Copenhagen Zoo. We strongly encourage you to contact with Anton Baotic, Department of Cognitive Biology, University of Vienna who has been in contact with the STDP in regards to recording devils in the free-range enclosures. The CRAG is in place to facilitate discussions between researchers to ensure that there is no duplication of effort on this program.

Please note if you are going to work in the free-range enclosures you will need to adhere to the DPIPWE OH&S requirements. These can be obtained from Drew Lee.

We wish you all the best in your proposed project and look forward to receiving your reports. If you have any questions or would like to discuss this further please feel free to contact me.

Kind regards

Dr Carolyn Hogg
CRAG Chair (Acting)

ANIMAL RESEARCH AUTHORITY (ARA)

MACQUARIE UNIVERSITY

AEC Reference No.: 2013/037   **Date of Expiry:** 31 October 2014

Full Approval Duration: *1 November 2013 to 1 January 2016 (26 Months)*

This ARA remains in force until the Date of Expiry (unless suspended, cancelled or surrendered) **and will only be renewed upon receipt of a satisfactory Progress Report before expiry (see Approval email for submission details).**

Principal Investigator:
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Associate Investigators:
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In case of emergency, please contact:
the Principal Investigator / Associate Investigator named above
Animal Welfare Officer - 9850 7758 / 0439 497 383

The above-named are authorised by MACQUARIE UNIVERSITY ANIMAL ETHICS COMMITTEE to conduct the following research:

Title of the project: **Developing the First Acoustic Library of Native Australian Mammals**

Purpose: **3 - Education**

Aims: **To develop the first Acoustic Library of Native Australian Mammals by collecting and preserving the vocal repertoires (with behavioural contexts) of native Australian mammals and developing an online database for conservation, education and scientific research**

Surgical Procedures category: 1 - Observation Involving Minor Interference

All procedures must be performed as per the AEC-approved protocol, unless stated otherwise by the AEC and/or AWO.

Maximum numbers approved (for the Full Approval Duration):

Species	Age/Sex/Weight	Total	Supplier/Source
38-44D : Native Mammals	Any	50	Taronga Zoo
38-44D : Native Mammals	Any	50	Australian Reptile Park
38-44D : Native Mammals	Any	50	Australia Wildlife Walkabout Park
38-44D : Native Mammals	Any	50	Wildlife Sydney
55A : Dingo / Wild dogs	Any	38	Colong Dingo Facility
41 : Dasyurids	Any	130	Devil Ark
	TOTAL	**368**	

Location of research:

Location	Full street address
Australian Wildlife Walkabout Park	Peats Ridge Rd., Calga NSW
Taronga Zoo	Bradleys Head Road, Mosman, NSW 2088
Australian Reptile Park	Pacific Highway, Somersby, NSW, 2250
Devil Ark	Barrington Tops, NSW
Colong Dingo Facility	Oberon, NSW
Wild Life Sydney Zoo	1-5 Wheat Rd. Sydney, NSW 2000

Amendments approved by the AEC since initial approval: N/A

Conditions of Approval: N/A

Being animal research carried out in accordance with the Code of Practice for a recognised research purpose and in connection with animals (other than exempt animals) that have been obtained from the holder of an animal suppliers licence.

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Professor Mark Connor (Chair, Animal Ethics Committee)   **Approval Date: 17 October 2013**

Adapted from Form C (issued under part IV of the Animal Research Act, 1985)
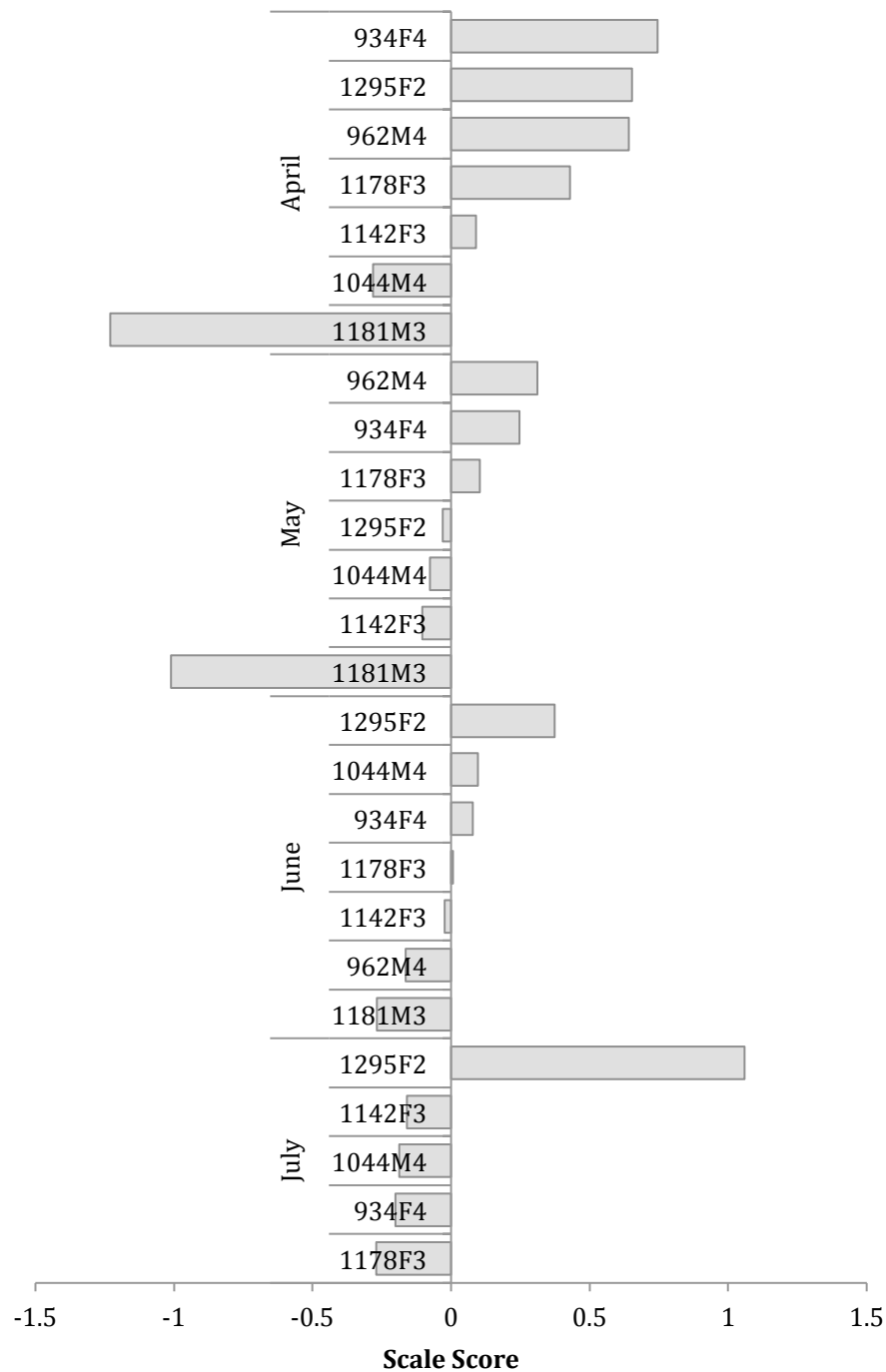
Appendix 3

Figure A1a. Scale scores calculated using the BBS method (Jameson et al. 1999) for the individuals in F3, Devil Ark, Barrington Tops, NSW, for the four observation periods (April-July). A negative score indicates that the number of encounters that an individual lost was greater than or equal to the number of encounters that the individual won. Conversely, a positive score indicates that the individual won more encounters than it lost. Individuals 962M4 and 1181M3 were not present for the July period as they were removed from the enclosure due to injury. There were no consistencies in the relative ranks of the individuals across the 4 months, although individual 1181M3 was consistently ranked lowest for the months where he was present in the enclosure.
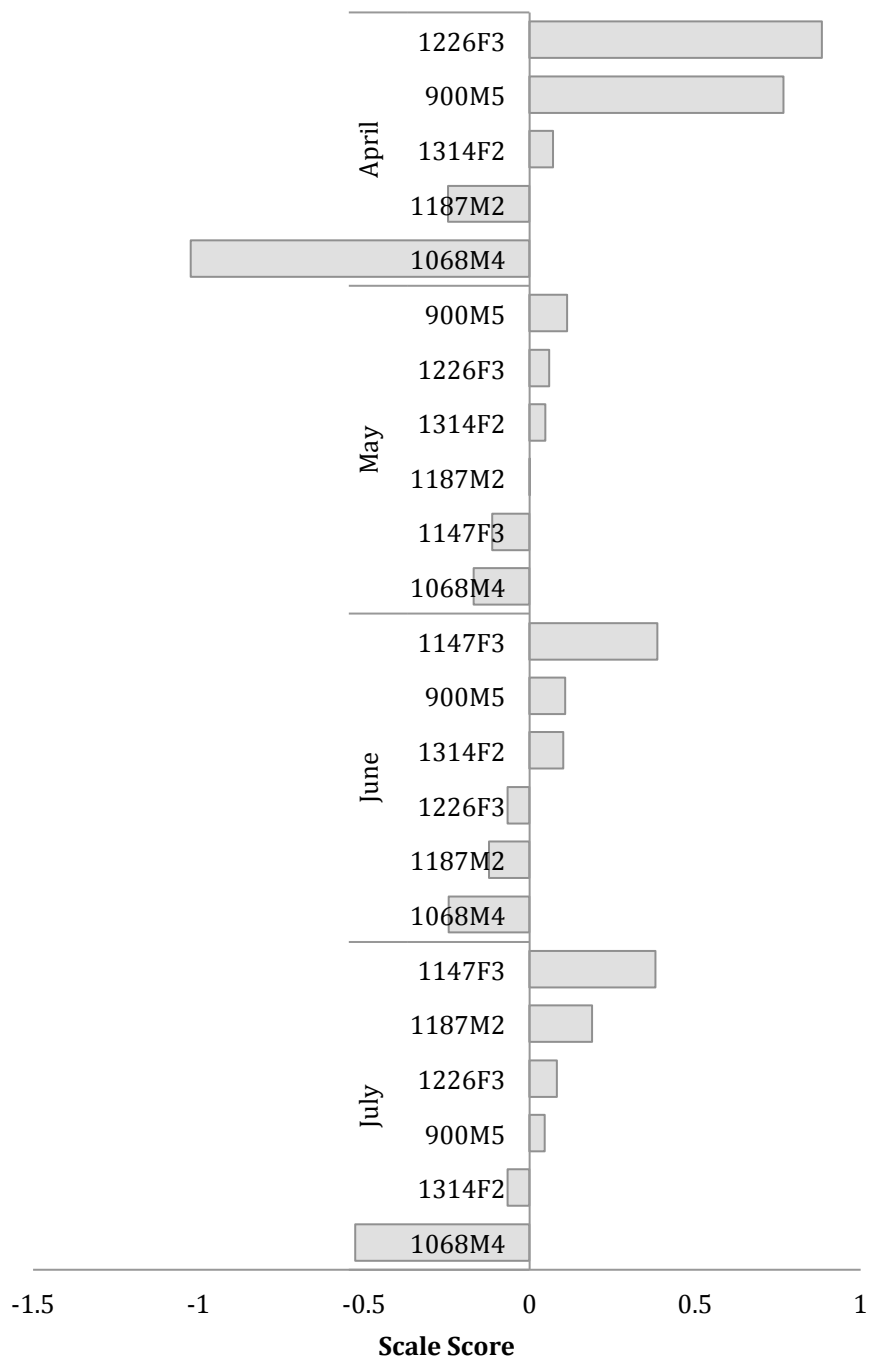
Figure A1b. Scale scores calculated using the BBS method (Jameson et al. 1999) for the individuals in F5, at Devil Ark, Barrington Tops, NSW, for the four observation months. A negative score indicates that the number of encounters that an individual lost was greater than or equal to the number of encounters that the individual won. Conversely, a positive score indicates that the individual won more encounters than it lost. Individual 1147F3, although present in the enclosure for all months, was not observed during the April group feeds, and therefore, her scale score for April could not be calculated. Individual 1068M4 was one of only two individuals across all enclosures to have a consistent rank (lowest) across the entire observation period.
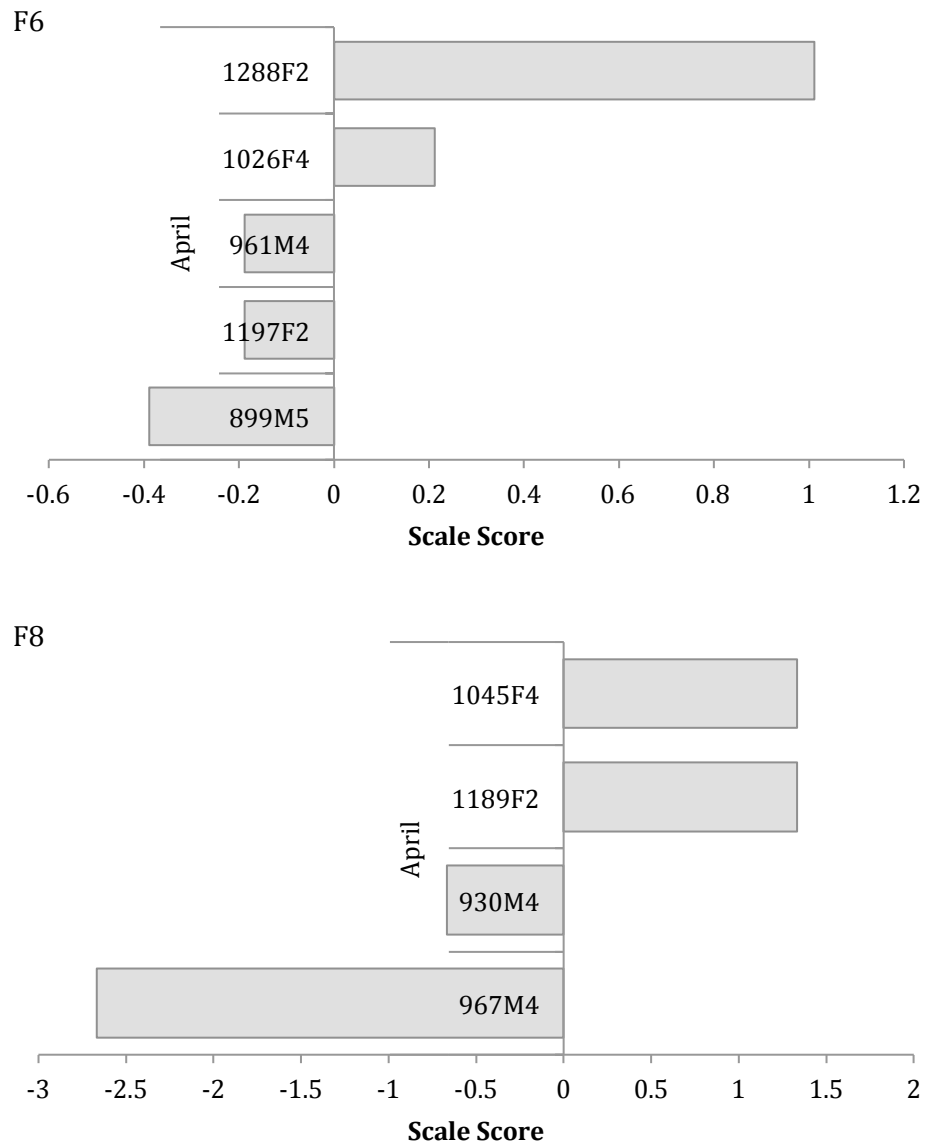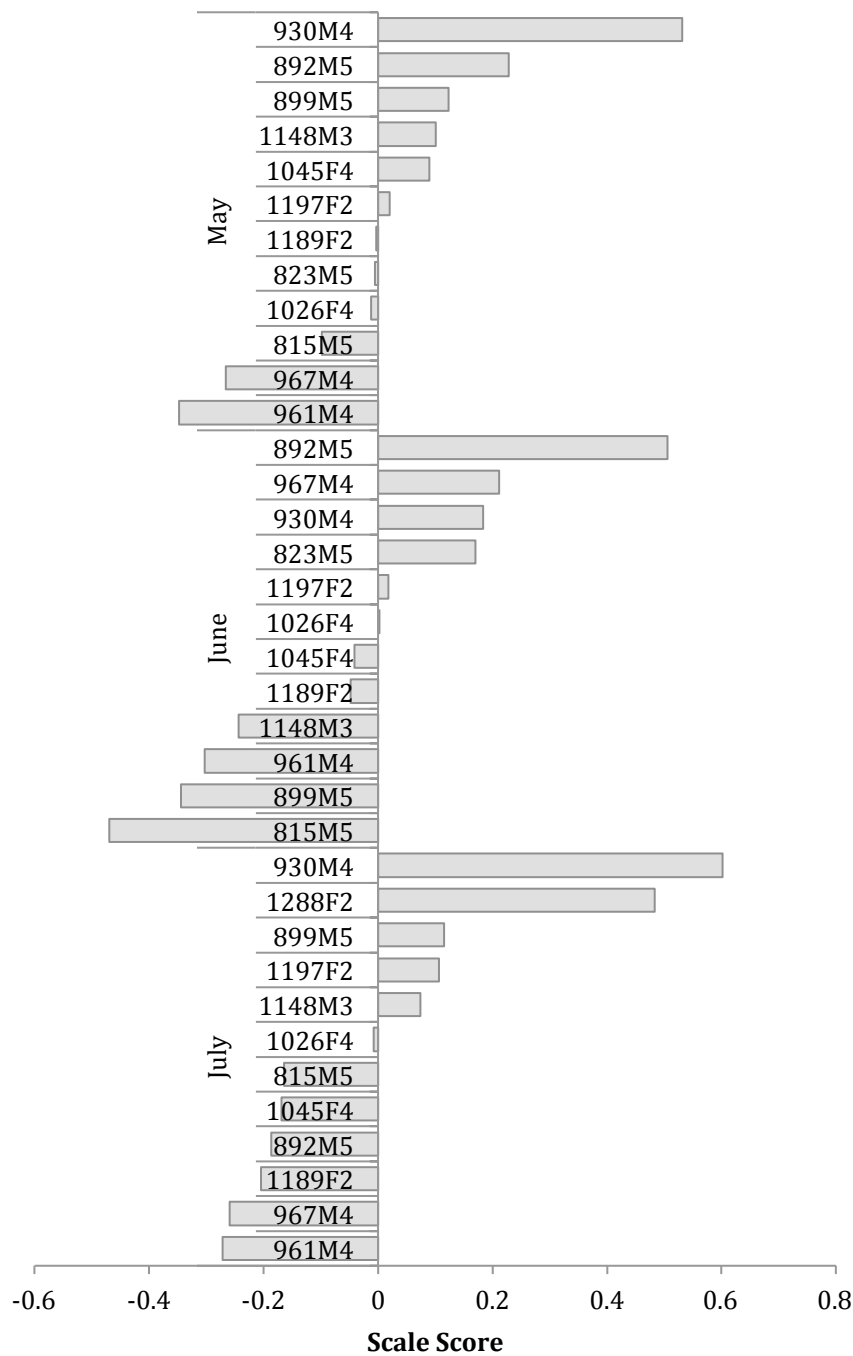
Figure A1c. Scale scores calculated using the BBS method (Jameson et al. 1999) for the individuals in F6 and F8, Devil Ark, Barrington Tops, NSW, for April. A negative score indicates that the number of encounters that an individual lost was greater than or equal to the number of encounters that the individual won. Conversely, a positive score indicates that the individual won more encounters than it lost. The scores for April for these two enclosures are presented separately from the other 3 months, as the enclosures were separate during this time. Comparisons of these scores to the relative ranks as shown in Figure A1d (below) showed no consistencies in ranks across the observation period (April-July). Individuals 815M5, 892M5, 1151F3 and 1148M3 were present in their respective enclosures, however, were never observed at the group feeds during the April recordings and therefore their scale scores could not be calculated for this month.

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Figure A1d. Scale scores calculated using the BBS method (Jameson et al. 1999) for the individuals in F6/8, Devil Ark, Barrington Tops, NSW, for the 3 months that enclosures F6 and F8 were joined (May-June). A negative score indicates that the number of encounters that an individual lost was greater than or equal to the number of encounters that the individual won. Conversely, a positive score indicates that the individual won more encounters than it lost. Individual 1151F3 was removed from the enclosure before the May recordings. Individual 823M5 was taken out of the enclosure for the July recordings and individual 1228F2 was only in the enclosure for the July recordings. For the individuals that were present for the 3 months that the enclosures were joined, there were no consistencies in their relative ranks.
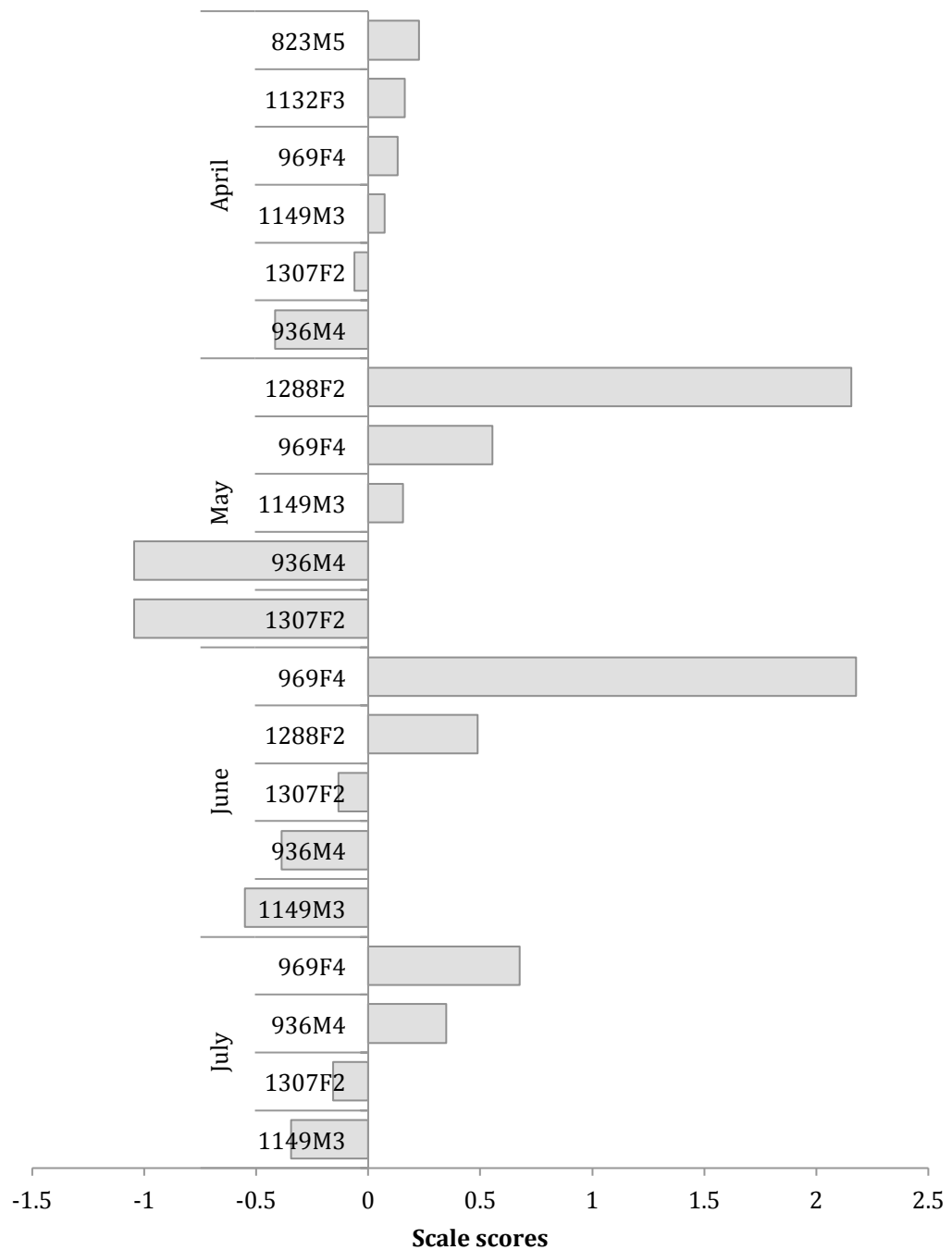
Figure A1e. Scale scores calculated using the BBS method (Jameson et al. 1999) for the individuals in F7, Devil Ark, Barrington Tops, NSW, for the four observation periods (April-July). A negative score indicates that the number of encounters that an individual lost was greater than or equal to the number of encounters that the individual won. Conversely, a positive score indicates that the individual won more encounters than it lost. Individuals 823M5 and 1096F3 were removed after the April period and individual 1228F2 was present in the enclosure for the May and June recordings. For the individuals that were present for the entire observation period, there were no consistencies in their relative ranks.
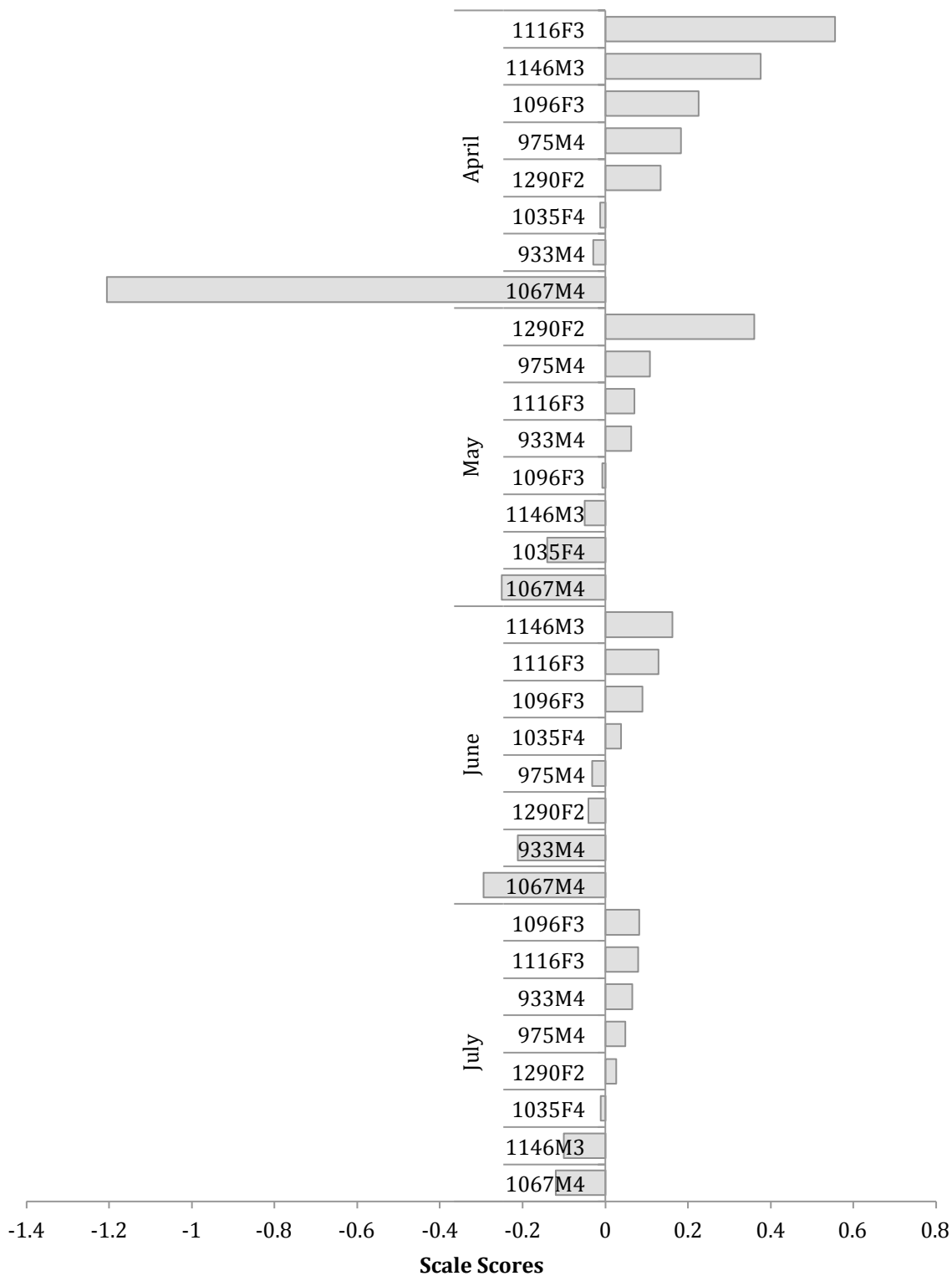
Figure A1f. Scale scores calculated using the BBS method for the individuals in F9, Devil Ark, Barrington Tops, NSW, for the four observation periods (April-July). A negative score indicates that the number of encounters that an individual lost was greater than or equal to the number of encounters that the individual won. Conversely, a positive score indicates that the individual won more encounters than it lost. Individual 1067M4 was one of only two individuals across all enclosures to have a consistent rank (lowest) across the entire observation period.