

How does relative refuge angle influence escape behavior: an empirical test with yellow-bellied marmots.

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Abstract

Flight initiation distance, or FID, is the distance between a predator and its prey at which the prey decides to flee. FID is influenced by several internal and external factors, which influence the potential costs and benefits of escape. For refuging prey, their path to a refuge may force them to get closer to the prey or permit them to flee the approaching predator. If the prey assesses the risk of fleeing towards a predator to be greater than when fleeing away from a predator, FID when fleeing towards a predator to a refuge would be expected to be larger. The relative position between predator, prey, and a refuge creates an angle called the relative refuge angle, or RRA. A recent model uses these variables to predict FID. Using yellow-bellied marmots (*Marmota flaviventris*), we evaluated the efficacy of this model in predicting FID, and then asked how much variation in FID was explained by RRA. We found, that although the model successfully predicted FID in our data, RRA had almost no effect on the overall variation in FID. Therefore, RRA may not be an important factor to marmots making escape decisions.

Introduction

When confronted by a predator, prey make escape decisions in a way that minimizes overall risk and maximizes benefits. In the 30 years since Ydenberg and Dill's (1986) ground-breaking model explaining the economics of escape behavior, there has been a considerable amount of work focusing on flight initiation distance (FID), or the distance at which a predator can approach prey before it flees (Cooper & Blumstein 2015). Indeed, two recent summaries of this literature (Cooper and Blumstein 2015; Samia et al. 2013) have shown multiple internal factors, such as stress hormone levels (Mateo 2007), body size (Caro 2005; Gotanda et al. 2009),

pregnancy (Braña 1993), reproductive opportunity (Cooper 1997, 1999), degree of habituation (Cooke 1980; Burger & Gochfeld 1983; Lord et al. 2001), and body condition (Bachman 1993), and external factors such as habitat type (Frid 1997), visibility (Ebensperger & Hurtado 2005), group size (Beauchamp 2008), time of year (Metcalf & Furness 1984), predator-approach velocity (Ydenberg & Dill 1986), distance to burrow (Dill & Houtman 1989), influence the decision to flee. Kramer and Bonenfant (1997) developed a model and demonstrated empirically the angle the prey must flee to the refuge can influence FID.

Relative refuge angle, or RRA, describes a prey's orientation to a discrete refuge relative to the path of a predator's approach. RRA influences FID, in that it indicates to what degree a prey must run towards or away from a predator to reach a refuge. It is expected that an animal fleeing towards a predator will have a larger FID than an animal fleeing away from a predator because an animal fleeing away from a predator assumes a smaller risk than an animal fleeing towards a predator (Cooper 2007). Kramer and Bonenfant (1997) tested this in a linear scenario in woodchucks (*Marmota monax*), where the predator, prey, and refuge were all along the same straight path, as detailed in **Figure 1**. Prey in front of a refuge relative to an approaching predator had a measured RRA of 0°, and would have to flee directly away from the predator to reach the refuge, while prey behind a refuge had an RRA of 180°, and would have to flee directly towards a predator. Prey with an RRA of 0° had smaller FIDs than prey with an RRA of 180° (Kramer and Bonenfant 1997), indicating that prey fleeing towards a predator assess a greater risk in fleeing to the burrow, and therefore flee sooner.

Cooper et al. (MS) extended this model to reflect the complexities of escape. In addition to including all angles when considering RRA, their model also recognizes that the prey's distance to the refuge, the predator's distance to a refuge, and RRA should all influence optimal FID. The

full model developed by Cooper et al. also factors in a predator's attack speed and a prey's speed of escape, but if these are held constant, the predator and prey's distance to the refuge and the RRA can be tested. Given these variables, FID can be predicted mathematically using the law of cosines for any angle around a refuge, not just the two linear scenarios described by Kramer and Bonenfant (Cooper et al. MS).

While the Cooper et al. model aims to predict FID over a wider range of scenarios than the Kramer and Bonenfant model, it still is based on the same behavioral constant, that a prey item will assess a larger risk in fleeing towards a predator than when fleeing away from a predator, resulting in a larger FID (**Figure 3.**).

In addition to evaluating the efficacy of the model in predicting FID, it is also important to estimate the relative importance of RRA in relation to other factors in explaining variation in FID. For this study, we focused on yellow-bellied marmots (*Marmota flaviventris*), a species well-suited to these FID experiments for their propensity to live in burrows, which provide a discrete unit of refuge when fleeing (Blumstein 1998; Blumstein et al. 2001), and a number of other prior studies of FID.

By conducting these field tests in marmots, we hoped to evaluate two questions. First, could Cooper et al.'s model accurately predict FID when RRA is measured? Second, relatively how important was RRA in explaining variation in FID when other factors known to explain variation in FID are taken into account?

Methods

Study System

We studied individually marked, adult yellow-bellied marmots in and around the Rocky Mountain Biological Lab in Gothic, Colorado (38.9592° N, 106.9898° W) at various colony locations (**Figures 4. and 5.**). These marmots were live-trapped, permanently marked with metal, numeric ear tags, and their dorsal pelage was marked with black Nyanzol dye to facilitate identification from afar (details in Blumstein 2013-Phil Trans).

Experimental Procedure

To estimate an FID, an individual marmot was identified by its fur dye mark from afar. After the individual was observed to be in a non-agitated state (it was standing and looking, lying down and looking, or foraging), the experiment commenced and the marmot was approached by a single person at a constant velocity of 0.5 m/s. Observers trained until their pace was $0.5 \text{ m/s} \pm 0.1 \text{ m/s}$. The observer dropped a flag when the marmot became alert (defined as a visible movement of its head – Cooper and Blumstein 2010), and dropped another flag when the marmot moved towards its burrow (defined as FID). The researcher then altered their course (if required) to continue walking directly at the subject until the animal has entered its burrow. At the burrow, and using a laser range finder, the observer measured the distance to the escape flag (FID), the distance to the alert flag (Alert Distance), and the observers' distance to the refuge at FID.

When we had more than a single observation on a subject, we selected those where the marmot was furthest from its burrow. We then asked two questions:

First, how well does the Cooper et al. (MS) model predict FID? To evaluate this, we used their key equation:

$$(FID)^2 = DR_{pred}^2 + DR_{prey}^2 - 2DR_{pred}DR_{prey}\cos(RRA),$$

where DR_{pred} is the predator's (the observer's) distance to the refuge, DR_{prey} is the prey's distance to the refuge, and RRA is the relative refuge angle (Cooper et al. MS), to predict a value for FID for each experiment. We then linearly regressed this against observed FID.

Second, how important is escape angle in explaining variation in FID? To address this, we fitted a General Linear Model to explain variation in FID. Our independent variables included: alert distance, because it explains considerable variation in FID (Blumstein et al. 2005; Samia et al. 2013; Samia and Blumstein 2014), colony site, because prior work has shown that marmots in our population that are differentially exposed to humans have different FIDs based on their exposure (Li et al. 2011), and RRA which tested the prediction of the Cooper et al. model in multiple ways. We can examine the significance of RRA in variation in FID in a simple GLM with alert distance and colony site. The significance of RRA can also be tested in regards to how it relates to the other components of the model, prey distance to burrow, and predator distance to burrow.

We log transformed FID and Alert Distance to meet the homogeneity of variance assumption of linear models. By doing so, the overall variance was homogeneous across distances. We forced our general linear models through the origin because logically, an alert distance of 0 could not have an FID greater than 0. All analyses were conducted in SPSS v. 23 (IBM SPSS v. 23), with alpha values set to 0.05. We used partial eta squares to measure effect size.

Results

Our final dataset contained 39 individuals, (26 adults, and 14 yearlings: 24 females, 15 males), that were flushed at 6 different colony sites. We found Cooper et al.'s model almost perfectly predicted marmot FID ($R = 0.975$; $p < 0.001$), with a relationship graphed in **Figure 4**. The

Cooper et al. model successfully predicted FID based on the distance the marmot was from its burrow, the distance the approaching human was from the marmot burrow when it initiated escape, and the escape angle with respect to the human. We then proceeded to determine how much of the variation in FID was explained by the relative refuge angle. While we found significant effects of colony ($p = 0.034$) and alert distance ($p < 0.001$) in the model evaluating the significance of RRA, detailed in **Table 1**, no significant variation in FID was explained by relative refuge angle as a continuous variable in relation to other factors influencing FID ($p = 0.810$).

Discussion

The Cooper et al. model predicts FID quite effectively, but RRA's significance in the overall framework of escape decisions made by the marmots we studied seems negligible. When one examines the geometry of the data, it becomes apparent that the model can predict these distances with accuracy because DR_{prey} in the data studied tends to be fairly small, with the mean DR_{prey} being only about 4 m. Therefore, DR_{pred} and FID will be very similar values, despite the angle, and when the Cooper et al. equation is used, predicted FID will also not be very different from DR_{pred} . This redundancy of sorts makes itself apparent in the GLM, where alert distance and colony site explained over 90% of the variation in FID in the data in models that test only the significance of RRA.

While Kramer and Bonenfant's initial model found significant effects of the relative refuge angle in determining FID, Cooper et al.'s model shows a limited effect of RRA, while still being able to accurately predict FID. Therefore, the data show that the other components of the model must have a significant effect on FID to explain the model's effectiveness. Indeed, when the other

components of the model (DR_{prey} and DR_{pred}) were tested in a general linear model (**Table 2.**) along with alert distance and relative refuge angle, we found a significant effect of DR_{pred} , or the predator distance to burrow, on observed FID ($p = 0.01$), while RRA's effect on observed FID remained insignificant ($p = 0.675$). This implies that, when making escape decisions, a predator's distance to a refuge is more important to marmots than whether or not they must flee towards or away from a predator. However, to truly evaluate this effect of DR_{pred} on FID, a wider range of values for each component of the model, specifically DR_{prey} , must be acquired.

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Table 1. Coefficient estimates, standard error (SE), significance (p), and partial Eta squared of the General Linear Model testing the main effects of Colony Site, Log Alert Distance, and a continuous measure of RRA on Log transformed FID. Bold values indicate significant effects.

Category	Estimate	SE	p
Colony Site			0.034
Bench/River	-0.079	0.162	0.631

Gothich Town	-0.263	0.142	0.074
Marmot Meadow	-0.045	0.183	0.807
Boulder/North Picnic	-0.274	0.175	0.127
Picnic	-0.095	0.159	0.557
Stonefield	-0.264	0.210	0.220
Log Alert Distance	0.985	0.097	<0.001
RRA	0.000	0.001	0.810

Table 2. Coefficient estimates, standard error (SE), significance (p), and partial Eta squared of the General Linear Model testing the main effects of Log Alert Distance, Relative Refuge Angle, the Predator Distance to Burrow, the Prey Distance to burrow, and the interaction between the components of the model on observed FID. Bold values indicate significant effects.

Category	Estimate	SE	P	Partial Eta Squared
Predator Distance to burrow	0.005	0.002	0.010	0.181
Prey Distance to Burrow	0.011	0.010	0.276	0.035
Relative Refuge Angle	0.013	0.031	0.675	0.005
Interaction Between Components of Model	<0.001	<0.001	0.354	0.025
Log Alert Distance	0.769	0.064	<0.001	0.810

Figures Legend

Figure 1. Diagram describing Kramer and Bonenfant's model of FID as it related to relative refuge angle (RRA) in two different scenarios. The left scenario has the prey in front of a burrow, with an RRA of 0° , while the right scenario has the prey behind a burrow with an RRA of 180° . The prey in each scenario are is the same distance from the burrow, but the prey in the right scenario has a larger FID since it must flee towards a predator.

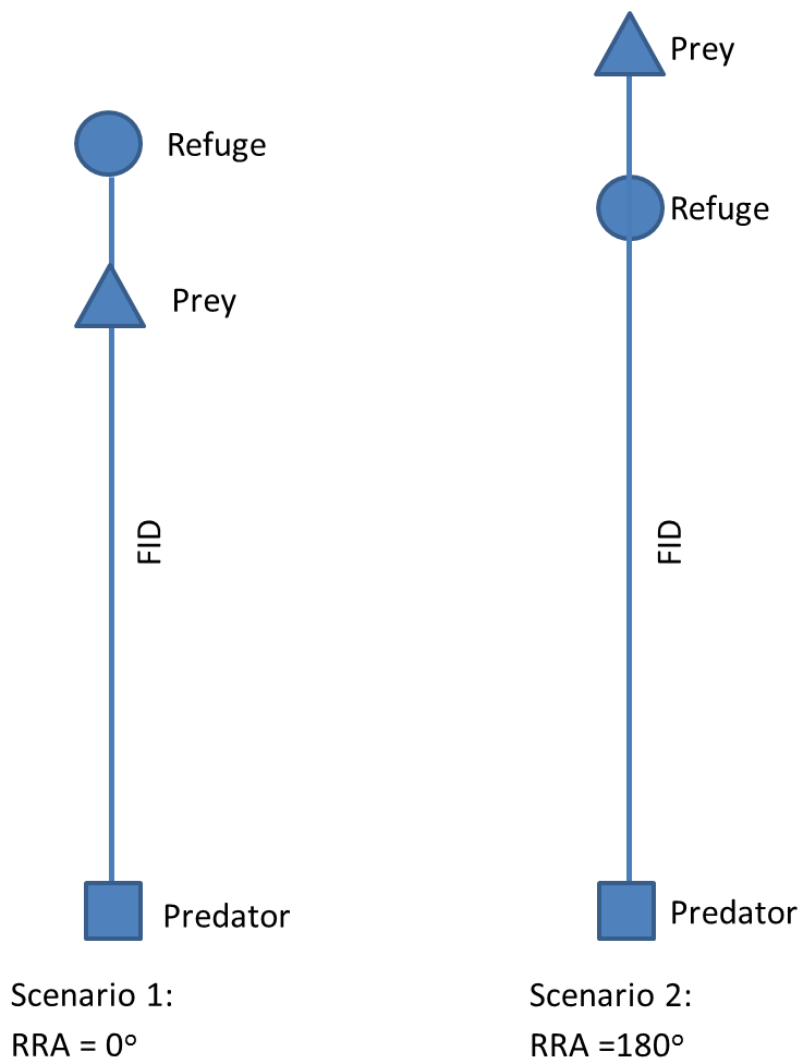


Figure 2. Diagram describing the geometry of the Cooper et al. (MS) model, and what values the observer will be measuring in the field, where DR_{pred} is the “predator’s” (observer’s) distance to the refuge, DR_{prey} is the prey’s distance to refuge, FID is the flight initiation distance, and RRA is the angle between DR_{prey} and DR_{pred} .

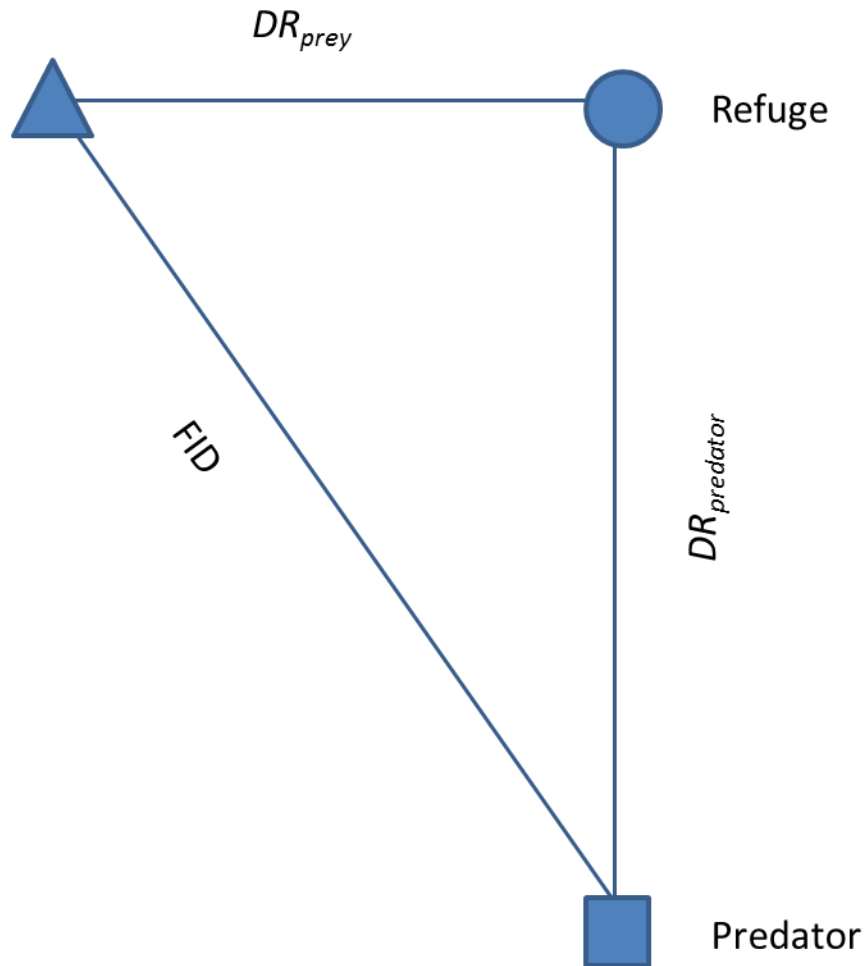


Figure 3. Diagram displaying the predictions made by the Cooper et al. (MS) model, and how it expands upon Kramer and Bonenfant's (1997) model. Prey with an angular position in Region 1 will have larger FID's than prey in Region 2.

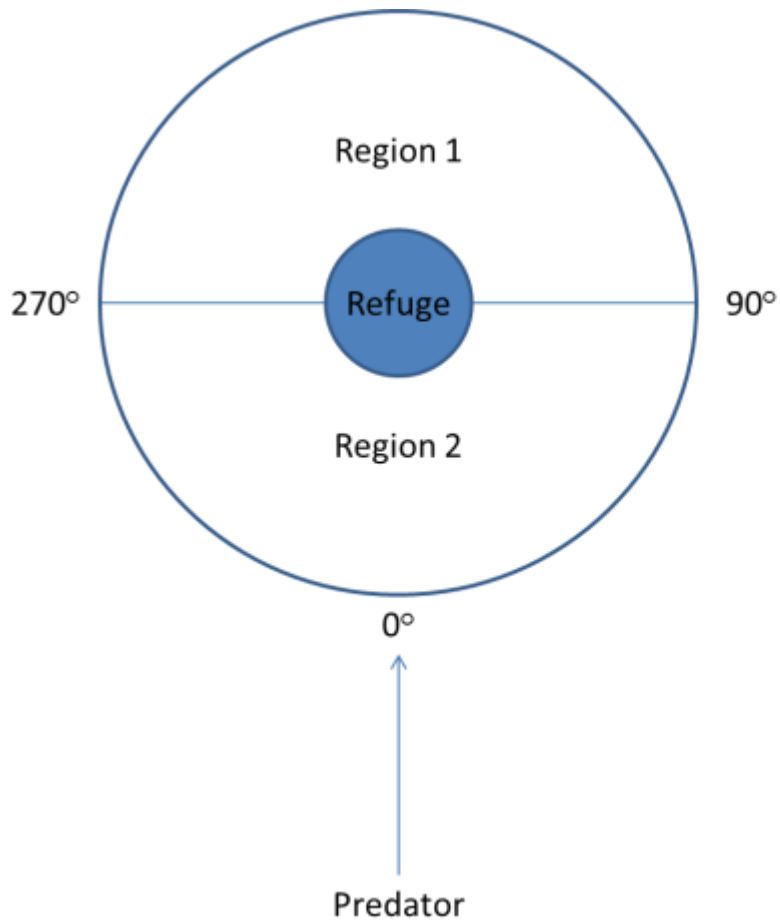


Figure 4. Map of colony locations in the southern portion of the valley.

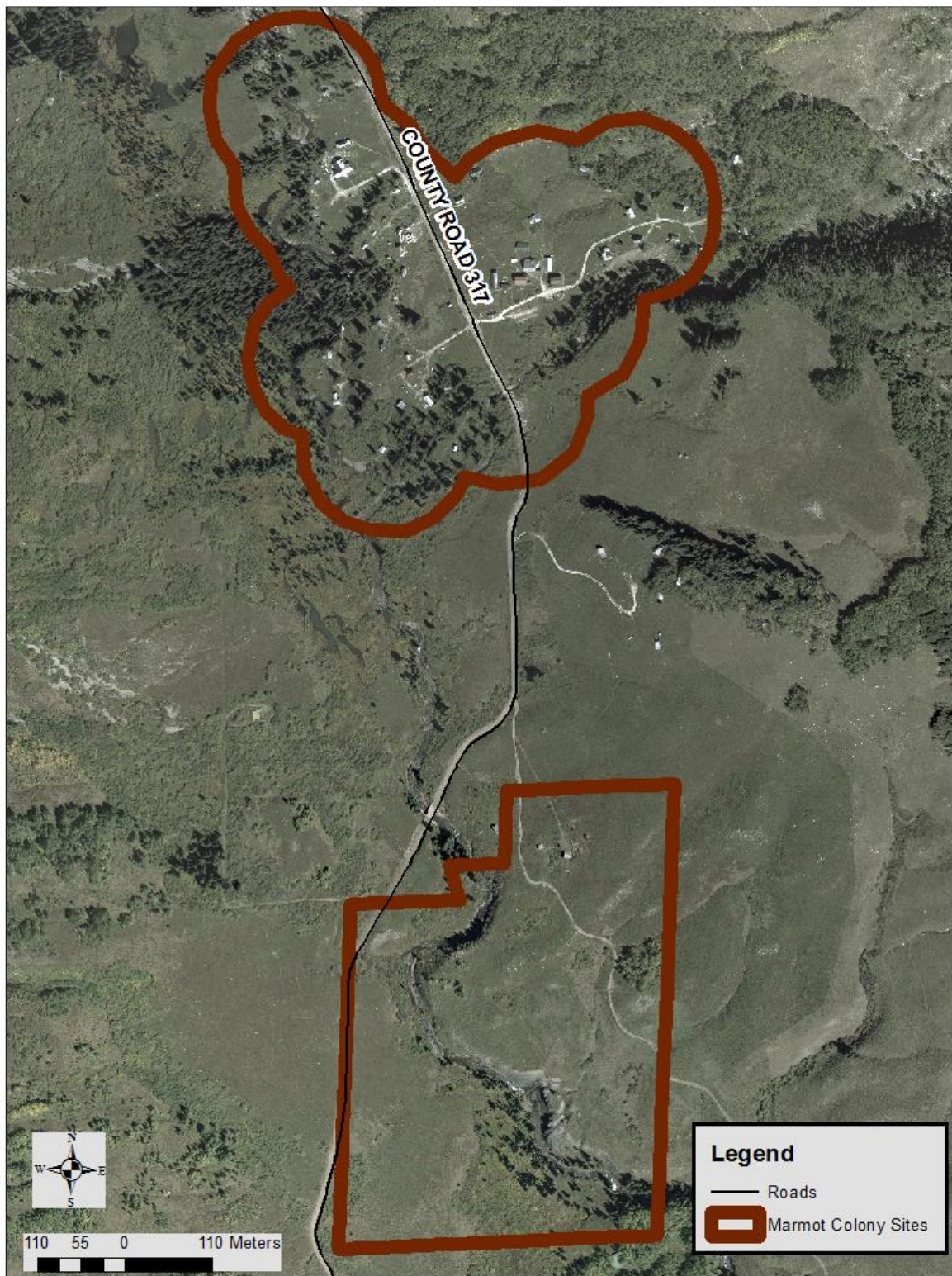


Figure 5. Map of marmot colony locations in the northern half of the valley.



Figure 6. Scatter plot displaying a linear regression of predicted FID vs. observed FID. The strong correlation ($R = 0.975$), indicates the Cooper et al. (MS) model effectively predicts FID in these data.

