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Running Head: CRAWFORD *ET AL.*—AGGRESSION IN BEAVERS

Conspecific Aggression by Beavers (*Castor canadensis*) in the Sangamon River Basin in Central Illinois: Correlates with Habitat, Age, Sex and Season

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ABSTRACT.— Conspecific aggression may play an important role in partitioning resources and maintaining territories among beavers (*Castor canadensis*), yet few studies have examined physical evidence of agonistic encounters. We trapped and examined pelts from 147 beavers harvested between 2006 and 2012 from the Sangamon River (n = 96) and tributary streams (n = 51) in central Illinois. We modeled the influence of sex, age class, season (predispersal or dispersal), and habitat (river or tributary stream) on the number of recent injuries caused by conspecifics. One-third (51/147) of beavers had ≥ 1 injury; of those, the median number of injuries was 2.0. Kits had fewer injuries than adults ($\beta_{Kit} = -2.24 \pm 0.63$), but yearlings and subadults did not ($\beta_{yearling} = 0.02 \pm 0.38$, $\beta_{subadult} = -0.22 \pm 0.48$). Beavers on small streams had

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only one-quarter of the injuries recorded for beavers on the river ($\beta_{Stream} = -1.34 \pm 0.82$). We failed to detect differences in injuries between the sexes. Our results suggest that both sexes participate in territorial defense through physical confrontations, and that such encounters can be costly to both dispersing juveniles and resident adults.

INTRODUCTION

Conspecific aggression plays an important role in partitioning resources and maintaining social order among beavers (*Castor canadensis*). These benefits entail risks to individuals because agonistic encounters can lead to injuries that reduce fitness or cause mortality (Svendsen, 1980; DeStefano *et al*., 2006). Svendsen (1980) noted bite wounds on two dispersing subadults and one kit that had died from bite wounds inflicted by an unrelated adult. Sun (2003) speculated that intercolony agonistic encounters were rare, but noted a lack of empirical evidence to support these views. Bradt (1938) suggested that subadults were actively driven from the colony by adults, but videos of beavers in dens have revealed few agonistic behaviors among colony members (0.1% of time-activity budget; Mott *et al*., 2011). Behaviors of beavers engaged in agonistic encounters (*e.g.*, pushing, lunging, sham-biting and biting; Bradt, 1938; Wilsson, 1971; Hodgdon, 1978; Hodgdon and Lancia, 1983) resemble those of rats (*Rattus norvegicus*; Takhashi and Blanchard, 1982), mice (*Mus musculus*; Litvin *et al*., 2007) and other rodents observed in captivity (Blanchard *et al*., 1979). Thus, it is reasonable to assume defensive strategies reduce the likelihood of injuries, most bites are inflicted on the back or other non-vital parts of an opponent, and few bites pierce the skin (Blanchard *et al*., 1979; Takhashi and Blanchard, 1982; Blanchard *et al*., 2003; Litvin *et al*., 2007).

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Behavioral adaptations also should reduce the incidence and severity of injuries caused by conspecific aggression. For example, scent marking reduces the incidence of agonistic encounters by advertising territorial boundaries, as does the ability to distinguish scents of kin and neighbors from those of strangers (Welsh and Müeller-Schwarze, 1989; Davis *et al*., 1994; Sun and Müeller-Schwarze, 1997, 1998; Rosell and Bjørkøyli, 2002; Herr *et al*., 2006). Territory-holding adults advertise their status and defend colony boundaries through scent marking, but they may be less likely to initiate aggressive attacks given that they risk losing their colony during such encounters. In contrast dispersing subadults searching for a colony may have little choice but to challenge territory-holders by overmarking and aggressive behavior (Tinnesand *et al*., 2013). Scent marking increases with increasing colony density, suggesting that beavers must spend more time defending territorial boundaries (Davis *et al*., 1994; Muller-Schwarze and Heckman, 1980). Accordingly we would expect aggressive encounters to increase with increasing colony density or along primary dispersal corridors. Therefore aggressive encounters may be more frequent in saturated or nearly saturated populations, in which juveniles make exploratory movements, but often fail to disperse (Havens, 2006; DeStefano *et al*., 2006; Bloomquist and Nielsen, 2010).

Common hypotheses regarding aggression and territoriality in beavers include: (1) males are more likely than females to engage in aggressive encounters; (2) dispersing subadults are more prone to attacks than residents of established colonies; (3) aggressive encounters are more likely to occur during the dispersal season; and (4) colonies with discrete, easily defended territories such as those on small streams are less prone to aggressive encounters than beavers inhabiting open systems such as large wetlands, lakes or rivers (Nordstrom, 1972; Müeller-Schwarze and

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Heckman, 1980; Davis *et al*., 1994; Baker and Hill, 2003, Tinnesand *et al.,* 2013). Most attempts to quantify aggressive behaviors of North American and European beavers (*C. fiber*) have relied on staged responses of residents to scents of intruders (Welsh and Müeller-Schwarze, 1989; Sun and Müeller-Schwarze, 1997, 1998; Rosell and Bjørkøyli, 2002; Herr *et al*., 2006, Tinnesand *et al.,* 2013). Reports of injuries caused by conspecific aggression are rare (*e.g*., Müeller-Schwarze and Schulte, 1999). To that end we examined pelts of beavers trapped in the Sangamon River Basin of central Illinois to identify injuries caused by agonistic encounters. Counts of injuries were used to test hypotheses about sex, age, habitat (main stem of Sangamon River or 1st-3rd order streams), and season (predispersal or dispersal).

METHODS

STUDY AREA

The Sangamon River originates in McLean County, Illinois. Its main stem flows 386 km before emptying into the Illinois River (Illinois Department of Natural Resources, 2000). This 7th order stream drains 14,985 km^2 (ca. 10% of the state; Illinois Department of Natural Resources, 2001). Sampling occurred on the main stem of the Sangamon River near Petersburg, Illinois as well as on 1st to 3rd order streams in a wider geographic area of the river basin (Fig. 1; 40°1′N, 89°50′W). We lacked data about densities of beaver in our study area, but assumed they were high, as in other parts of the state (0.1–0.6 colonies/km of stream; Woolf *et al.,* 2003; Cox and Nelson, 2009).

CAPTURE AND HANDLING

We set body-gripping traps (25.4 x 25.4-cm frame) at artificial scent mounds, dam crossovers, channels and den entrances (Baker and Dwyer, 1987) during legal trapping seasons

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in Illinois (5 Nov – 31 Mar; 2006–2012). Traps met standards for animal welfare (American Veterinary Medical Association, 2007; Association of Fish and Wildlife Agencies, 2007; Gannon *et al*.,2007) and limited the likelihood of conspecific attacks on captured individuals (*e.g.*, McKinstry and Anderson, 1998; McNew *et al*., 2007). We classified captures before 20 Jan. as “predispersal”; all others (20 Jan. – 31 Mar.) were considered “dispersal” captures. January 20 was the earliest observed date of a permanent dispersal for 60 beavers monitored with radiotelemetry in the Embarras River watershed in east-central Illinois (Cleere, 2005; Havens, 2006).

We removed pelts from beavers as described by Hall and Obbard (1987), labeled them and placed them in a freezer for processing at a later date. Examination of exposed genitalia allowed us to determine sex (Osborn, 1955). Heads were separated from carcasses, placed in plastic bags, labeled and frozen. We allowed pelts to thaw, removed the hypodermis with a fleshing knife, and nailed perimeters of pelts to plywood to expose the entire surface of the dermis (Hall and Obbard, 1987). Crescent-shaped injuries caused by incisors of beavers were easy to identify (Fig. 2). We counted each injury that was caused by a pair of incisors passing entirely through the dermis. This included injuries where one of the incisors pierced the dermis but the other did not. Our narrow definition of an injury assured consistent counts when wounds were severe or too clustered to differentiate bites that caused them. For example, a single gaping wound with marks left by five pairs of incisors around its perimeter was tallied as five injuries. Skinner and Skinner (2008) used a similar approach to gauge aggression in muskrats (*Ondatra zibethicus*). Our counts were biased (*i.e.*, underestimates) because they did not include superficial wounds, those that had healed or those on extremities. Counts represented recent

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agonistic encounters with the most potential for severe consequences (*e.g.*, reduced fitness or mortality). We did not attempt to classify individual wounds by size or severity because we lacked objective scales and reasonable links to outcomes.

We boiled skulls in a pressure cooker for 1-2 h and separated lower jaws from skulls. Later we removed teeth from a lower jaw and assigned age classes based on development of the pre-molar and molars (van Nostrand and Stephenson, 1964; Larson and van Nostrand, 1968). As in other studies other studies in Illinois (McTaggart and Nelson, 2003; McNew and Woolf, 2005), we used four age classes: 0–12 mo (kit), 13–24 months (yearling), 25–36 mo (2 y old) and $\geq$ 37 mo (adult).

DATA ANALYSIS

We used general linear models with a negative binomial error distribution and log link to model the influence of habitat and demographic factors on the number of injuries recorded for each beaver because our counts of injuries did not fit a Poisson distribution (Zuur *et al.*, 2008). Categorical factors included the sex and age class of the beaver (as defined above), the season in which it was captured (predispersal or dispersal), and the habitat where it was captured (mainstem of Sangamon River or tributary stream). Beta coefficients for each level within factor were compared to the reference level specified for that factor. Adult females captured from the main river during the dispersal season served as the reference case in all models. We evaluated all plausible candidate models, including those with interaction terms, and ranked models by AICc (corrected for small sample size). Model fit was evaluated by graphical examination of residuals versus fitted values. Parameters were averaged from models that were within 2 AICc units of the top model (Burnham and Anderson, 2002). All statistical procedures were carried

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out in the R programming language (R Development Core Team, 2013) using the package 'MASS' (Venables and Ripley, 2002).

RESULTS

We examined pelts from 147 beavers captured from the Sangamon River (n = 96) and tributary streams (n = 51). This sample consisted of 76 males and 71 females classified as kits (n = 38), yearlings (n = 48), subadults (n = 24), and adults (n = 37). Approximately equal numbers of individuals were harvested before (n = 74) and after (n = 73) the onset of the dispersal period. However our sample during the dispersal season was strongly biased towards beavers captured on the main river (64 of 73 captures).

Recent injuries were detected in 50 of 147 (34%) beavers. Of these, 19 (38%) were trapped during the predispersal period; the remaining 31 (62%) were trapped during the dispersal period. Only 16% of beavers trapped from smaller streams had injuries, whereas 44% of beavers from the river had ≥ 1 injury. The median number of injuries for beavers that had ≥ 1 injury was 2.0 (range: 1-26 injuries), and did not differ between males and females. Excluding two subadults that had 16 and 26 injuries, the number of injuries/beaver ranged from 1 to 8, with a mean of 2.60 (SD = 1.93).

The four most competitive models included age class, season of capture, and the habitat in which the beaver was captured (Table 1). Only one lower ranking model included sex, indicating that this factor had only a weak influence on number of injuries [$\beta_{Male} = 0.32 \pm 0.32$ (SE throughout), 95% CI = -0.32 – 0.96]. Kits were ten times less likely to have injuries than adults [Fig. 3; $\beta_{Kit} = -2.24 \pm 0.63$, CI = -3.51 – (-1.03)]. We failed to detect differences in number of injuries between yearling and subadult age classes and adults ($\beta_{yearling} = 0.02 \pm 0.38$,

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CI = -0.73 – 0.78; $\beta_{subadult}$ = -0.22 ± 0.48, CI = -1.18 – 0.70). Beavers occupying 1^{st}-3^{rd} -order streams had only one-quarter of the injuries recorded for beavers on the river [Fig. 4; β_{Stream} = -1.34 ± 0.82, CI = -1.84 – (-1.27)]. We failed to detect an effect of season on the number of injuries recorded ($\beta_{Predispersal}$ = -0.47 ± 0.41, CI = -1.26-0.38). The second competitive model included a habitat x dispersal interaction ($\beta_{Stream\ x\ Predispersal}$ = 1.87 ± 1.15, CI = -0.39 – 4.15), but confidence intervals overlapped 0.

DISCUSSION

We made the assumption that injuries were the result of confrontations between territory holders and intruders, rather than the result of conflict within the colony. We believe this is a reasonable assumption given that little evidence exists for aggressive behavior among colony members (Baker and Hill, 2003). In addition attacks serious enough to cause the severe injuries recorded in this study are unlikely to come from relatives with a vested interest in offspring fitness. Adults may threaten their offspring during feeding (Busher, 1983; Baker and Hill, 2003), but such encounters are rare (Mott *et al*., 2011) and unlikely to result in injuries caused by injuries. Thus it is reasonable to assume that injuries were incurred during fights over territory.

We failed to detect differences in the incidence of injury between males and females, suggesting that both sexes participate in territorial defense. Intuitively males and females would encounter similar risks of agnostic encounters because they engage in many of the same activities (e.g., dam and lodge maintenance, food acquisition, and scent marking; Svendsen 1980) and have similar home range sizes, dispersal movements, and activity patterns (Svendsen 1980; DeStefano *et al*., 2006; Bloomquist and Nielsen, 2010, Havens *et al*. 2013). Our findings supported this view and were consistent with those of Herr *et al*. (2006), who reported both sexes

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responded aggressively to scents of simulated intruders. On the other hand, Müller-Schwarze and Schulte (1999) found more evidence of agonistic encounters in males (63%) than in females (37%) with ≥1 tail scar. Demographic, environmental and methodological differences among studies might explain disparities in findings.

Injuries to kits were rare in the Sangamon River Basin. Kits remain close to the lodge and play subordinate roles in the social hierarchy of the colony (Svendsen 1980), thereby reducing their risk of injuries due to aggressive encounters with dispersing strangers. Müller-Schwarze and Schulte (1999) never found tail scars on kits in their study, and this is consistent with our finding of only four kits with one injury each. Observations of colony activity suggest that kits remain close to the lodge in the first year of life, and do not engage in lodge maintenance, food acquisition, or scent marking (Svendsen, 1980).

We expected dispersing subadults to have more injuries than other age classes, especially for beavers captured during the dispersal season. Yet we did not find differences in the number of injuries between adults and other age classes, as was reported by Müller-Schwarze and Schulte (1999). In contrast we found that 46% of adult beavers had ≥ 1 injury, comparable to Müller-Schwarze and Schulte (1999), who found that > 50 % of adults had ≥ 1 tail scar. This is unsurprising given that territory-holding adults engaged in agonistic encounters with dispersing subadults would receive as well as deliver injuries.

Yearling beavers also did not appear to differ from adults in their frequencies of injuries, suggesting that yearlings are dispersing, and encountering territory holders, at similar rates as subadults in this region. In fact yearling dispersal is common in other beaver populations in Illinois (Cleere, 2005; McNew and Woolf, 2005; Havens, 2006; Bloomquist and Nielsen, 2010).

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Tinnesand *et al.* (2013) suggested that dispersing 2 y olds are more prone to aggressive encounters than adults with established territories. This seems reasonable, but unlike in northern latitudes, yearlings are also likely to disperse in Illinois. We believe that aggressive encounters pose risks of injury to both defenders and transgressors of territorial boundaries, so differences in social status do not confer a clear advantage for one party or the other.

Related to our expectations regarding age and injuries, we hypothesized that beavers captured after the start of the dispersal period (20 Jan) would have more injuries than those captured earlier in the winter. Although two of our most competitive models suggested that fewer injuries were incurred during the predispersal period, the model-averaged beta coefficient was associated with a large standard error. This may be due to the date that we chose to demarcate pre- and dispersal periods. The timing of natal dispersal varies according to individual, age, region, habitat availability, and other environmental factors (Baker and Hill, 2003; Cleere, 2005; McNew and Woolf, 2005; Havens, 2006; Bloomquist and Nielsen, 2010). Moreover, the lack of differences in injuries between periods may reflect predispersal exploratory movements during which subadults had the opportunity to physically challenge adult territory holders prior to permanent dispersal. Such exploratory movements have been observed in other beaver populations (Hodgdon, 1978; Havens, 2006).

We expected beavers on smaller streams to have fewer injuries, reflecting a better ability to mark and defend discrete territories, as well as the reduced traffic from dispersers on tributaries compared to the main river. Habitat was an important predictor in our models, but we also note that 88% of beavers captured during the dispersal period came from the main stem of the river. These skewed data reflect differences in trapping opportunities caused by logistical and practical

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constraints. For example ice hindered trapping on small streams earlier in the fall and later in the spring compared to the main river. Ice cover also might limit movements of beavers outside their territories (and therefore the probability of aggressive encounters). Before the dispersal period, beavers on small streams had fewer injuries than those on the main river; however, we are cautious to draw conclusions because of the relatively small predispersal sample size.

Attempts to characterize aggressive behaviors of beavers have relied mostly on casual observations and staged responses to scents of strangers. Our study was one of two that evaluated injuries caused by aggressive encounters with conspecifics. Overall injuries that pierced the dermis of beavers inhabiting the Sangamon River Basin were low in prevalence (34% of individuals) and intensity (median = 2.0 per individual with $\geq$1 injury). Our findings support the importance of behavioral strategies to reduce incidence of injuries (*e.g.*, scent-marking to advertise territorial boundaries; Baker and Hill, 2003) and their severity in beavers and other rodents (*e.g.*, submissive and defensive postures during aggressive encounters; Blanchard *et al.*, 1979; Litvin *et al.*, 2007). Müller-Schwarze and Schulte (1999) concluded that males are more likely to engage in aggressive encounters than females. Our findings differed, possibly because of methodological approaches for evaluating aggression, demographic and environmental influences on aggression, or our ability to test for effects with a large sample of both sexes.

Our most competitive models suggested differences in injuries between beavers inhabiting the main stem of the Sangamon and its tributaries, where territories are theoretically better defined and easier to defend. However differences in the duration of ice cover between the main stem and tributaries could have affected risks of agonistic encounters by limiting movements of beavers, as well as our ability to collect samples.

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Our study is one of only two studies to examine physical evidence of conspecific aggression in beavers. Injuries were relatively rare, but our estimates are conservative because we only tallied recent injuries. This methodology allowed us to examine differences between pre- and dispersal seasons, rather than assess cumulative injuries throughout the life of the beaver. If old scars could be confidently identified, such an analysis would allow researchers to examine differences between sexes and habitat more completely than our snapshot sampling protocol allowed. Yet our snapshot approach still captured differences in injuries between habitat types. Although estimates presented here are biased low, our methodology is appropriate for examining relative differences in conspecific aggression between beavers. We recommend continued research on conspecific aggression in other beaver populations to more fully examine the relative importance of colony density, spatial arrangement of colonies, and other environmental factors on conspecific aggression.

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Table 1.— Model selection results of negative binomial models used to model the number of injuries detected upon necropsy for beavers trapped from the Sangamon River and (*n* = 96) and tributary streams (*n* = 51) in central Illinois during 2006. For brevity, only models within 3 AIC_c units of the top model are shown; *k* is the number of parameters in the model and w_i/w_j is the relative weight of the model out of the candidate set (*n* = 36). All candidate models were used to estimate model averaged parameters and standard errors.

Model	*k*	AIC_c	ΔAIC_c	w_i/w_j
Age + Habitat	5	335.8	0.00	0.244
Age + Habitat + Dispersal + Habitat × Dispersal	7	336.9	1.16	0.137
Age + Habitat + Sex	6	337.0	1.25	0.131
Age + Habitat + Dispersal	6	337.4	1.59	0.110
Age + Habitat + Dispersal + Sex + Habitat × Dispersal	8	338.3	2.52	0.069
Age + Habitat + Dispersal + Sex	7	338.7	2.93	0.056

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FIG. 1.—Sampling locations for American beavers (*Castor canadensis*) along the main stem of the Sangamon River and tributaries in central Illinois.

FIG. 2.— Crescent-shaped injury caused by incisors of American beavers (*Castor canadensis*) during conspecific aggression

FIG. 3. —The mean (+ SE) number of injuries due to conspecific aggression according to age class for beavers trapped within the Sangamon River (*n* = 96) and tributary streams (*n* = 51) in central Illinois. Two subadults with 16 and 26 injuries each are not included in mean estimates. Beavers without any injuries were not included in the calculation of means. Sample size within each class is listed in parentheses

FIG. 4. —Frequency of injuries due to conspecific aggression detected in beavers trapped along the main channel of the Sangamon River (*n* = 96) and tributary streams (*n* = 51) from tributary streams in central Illinois

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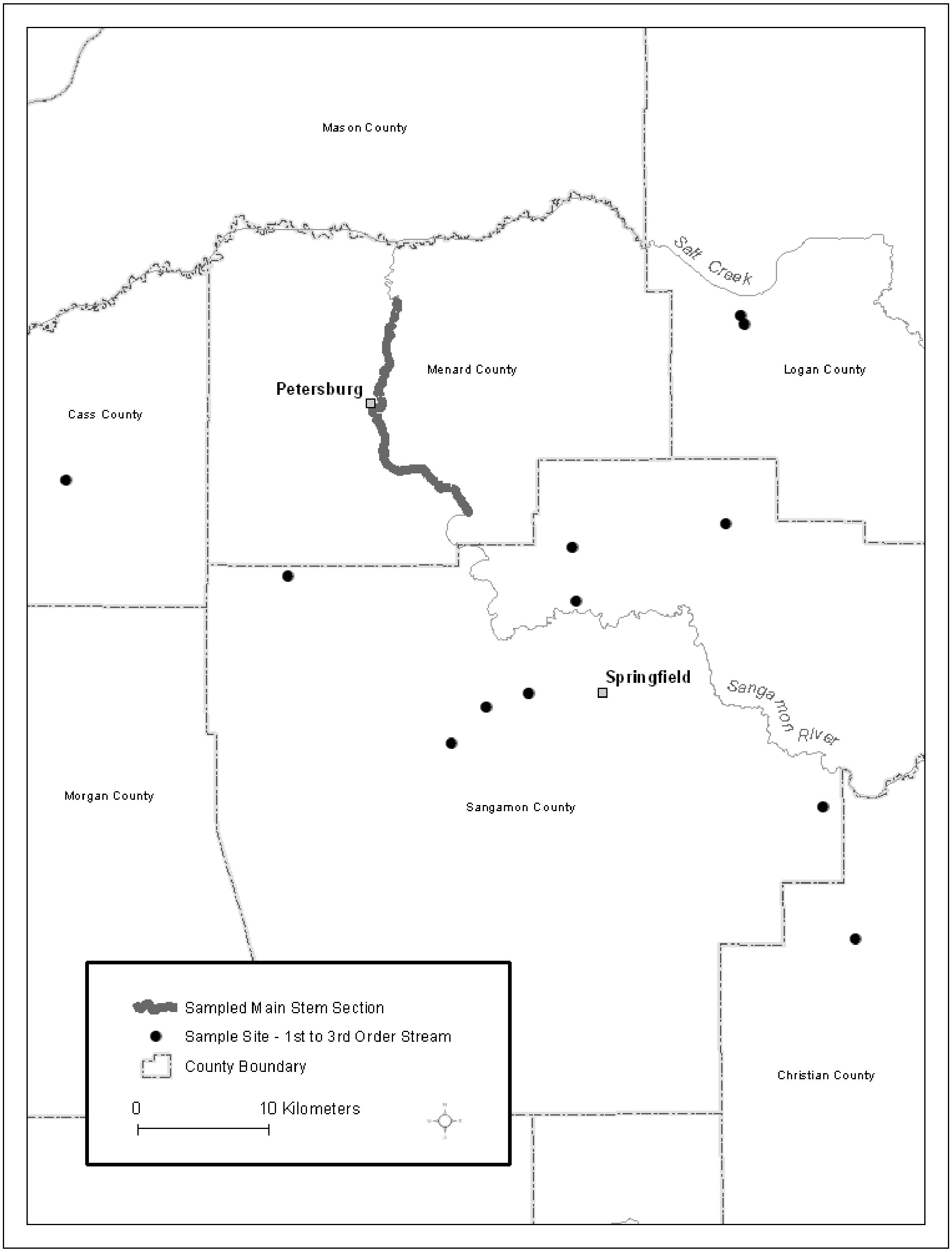

427

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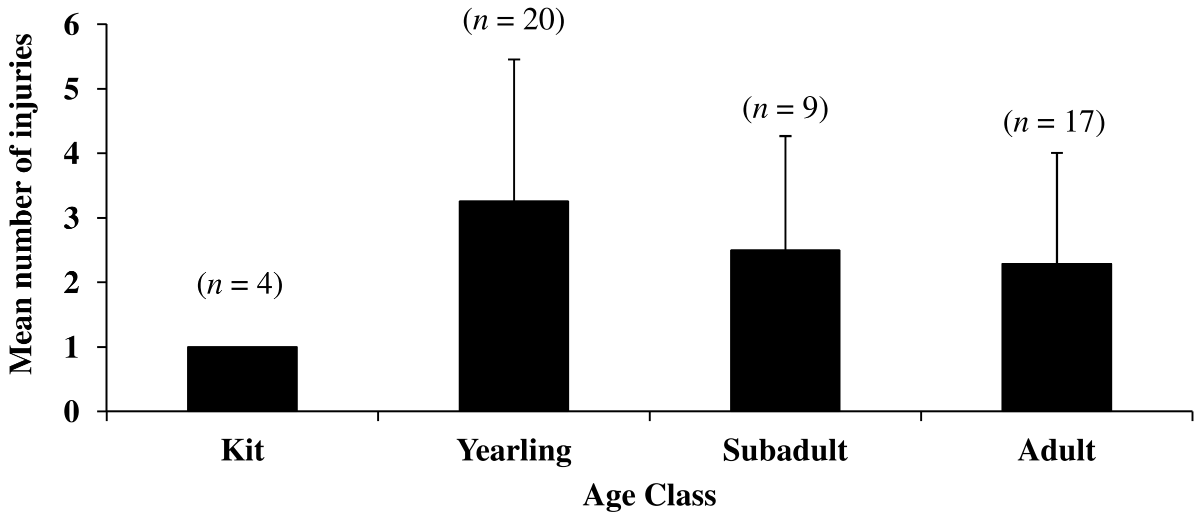

430

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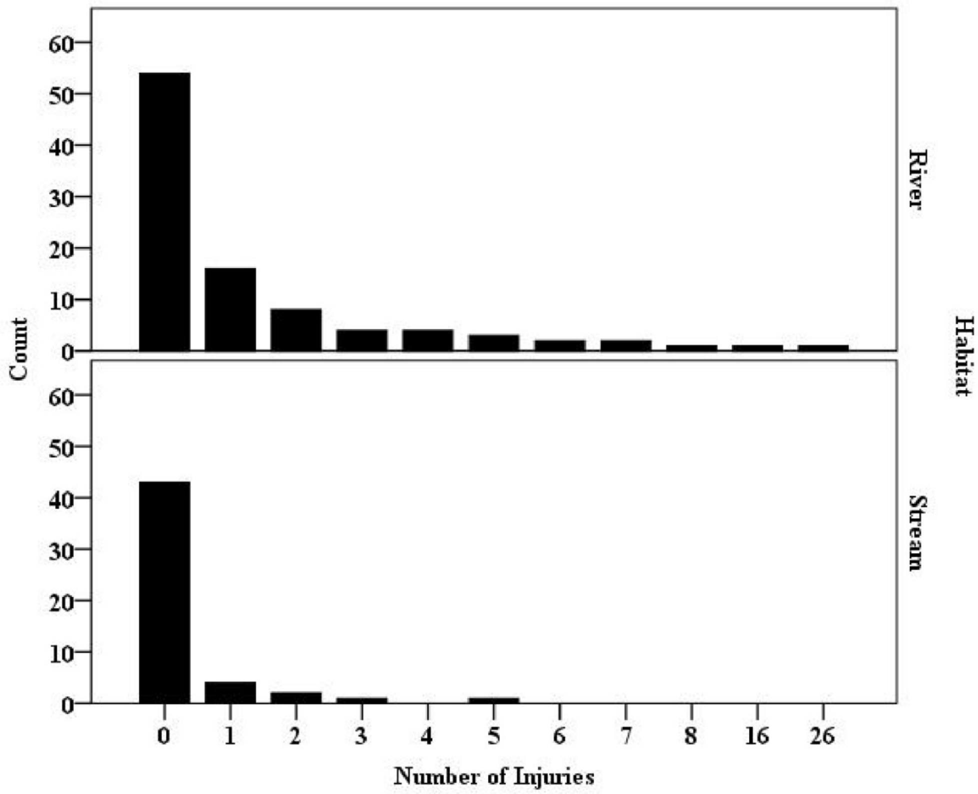
431



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