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Article

Direct Field Observation of Aggressive Behavior by a Rabid Big Brown Bat (*Eptesicus fuscus*) toward a Conspecific in Northern Arizona

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Abstract: Although aggressive behavior is a recognized manifestation of furious rabies, direct observations of aggressive interactions among free-ranging bats are uncommon because bats are nocturnal, highly mobile, and difficult to observe continuously. We report a direct observation of agonistic behavior by a male big brown bat (*Eptesicus fuscus*) towards another big brown bat during daylight hours on 30 June 2009 in northern Arizona, USA. The aggressive bat vocalized audibly while flying, then chased and attacked another big brown bat, attaching to the non-aggressive bat and maintaining a bite to its lower jaw during the interaction. The bats landed on the bole of a ponderosa pine tree (*Pinus ponderosa*), after which both bats fell to the ground. The attacking bat remained grounded and was captured and euthanized because of its unusual behavior and inability to fly. Brain tissue from this bat subsequently tested positive for rabies virus antigen using direct fluorescent antibody (dFA) testing. The event occurred during the maternity period and at a water source supporting high numbers of bats, conditions that can increase contact rates among individuals. This observation documents prolonged aggressive biting between two free-ranging big brown bats, one of which was laboratory-confirmed rabid, and illustrates how concentrated resources may provide opportunities for contact and rabies transmission. These observations suggest that seasonal aggregation and resource concentration may influence opportunities for rabies transmission and spillover in arid environments.

Keywords: aggression; behavior; Chiroptera; *Lyssavirus*; rabies; transmission

1. Introduction

Rabies is a fatal zoonotic disease caused by rabies virus (RABV; genus *Lyssavirus*, family *Rhabdoviridae*) and occurs globally [1–4]. Although all mammals are susceptible to infection, bats and wild mesocarnivores are important reservoirs of RABV in North America. Transmission occurs primarily through the introduction of virus-containing saliva into tissue, most often through the bite of an infected animal, and both intra- and interspecific transmission can occur [5–7]. Bats are particularly important hosts in the ecology of rabies because distinct RABV lineages are associated with different bat species, and social behavior and the highly mobile nature of bats can facilitate transmission, especially given the potential interaction with conspecifics and other species [8,9]. Social behaviors, including colonial roosting, grooming, and other close-contact interactions provide opportunities for repeated contact among individuals; seasonal movements and aggregation at concentrated resources can also affect patterns of contact among bats and between bats and other mammals [5]. Consequently, understanding the

behavioral and ecological circumstances associated with biting and other close-contact interactions can provide insight into rabies transmission and potential spillover [10].

Rabies can manifest through a variety of neurological and behavioral means in infected individuals [11]. The two clinical forms of the disease have been described as either an encephalitic form (furious) or a paralytic form [12]. The encephalitic form is characterized by altered activity, aggression, and biting while the paralytic form results in progressive motor impairment [3,13,14]. These expressions are not necessarily discrete; behavioral expression can vary among individuals, host species, and viral variants [7]. There are at least 16 distinct viruses in the lyssavirus genus that have been associated with mammalian reservoir hosts, predominantly bats and carnivores [15].

Among bats infected with rabies, reported clinical signs included unusual daytime activity, motor impairment, lethargy, grounding, and changes in social behavior. In captive colonies of big brown bats, rabies infection was associated with increased aggression, vocalization, and salivation in some individuals [13,16,17]. In experimental studies of captive big brown bats, infected individuals showed limited excretion of virus in their saliva and bat-to-bat transmission of RABV was not detected [18]. Similarly, Cárdenas-Canales et al. [19] tested an oral rabies vaccine in captive common vampire bats (*Desmodus rotundus*) and observed that rabid bats reduced social behavior (allogrooming) prior to death; however, no increase in aggression was noted. This demonstrated that variation in behavioral responses among rabies-infected bats.

Aggressive interactions between bats have also been documented under free-ranging conditions. Sasse et al. [20] documented a rabid eastern red bat (*Lasiurus borealis*) attached to an evening bat (*Nycticeius humeralis*) in Arkansas, providing direct evidence of interspecific aggression by a rabid bat. Bell [21] described aggressive encounters between bats that might be attributed to rabies infection in which a hoary bat (*Lasiurus cinereus*) pursued, attacked and grasped a bat, then fell to the ground with it during three separate interactions. The first two occurred during daylight, and he was able to identify that the hoary bat attacked a silver-haired bat (*Lasionycteris noctivagans*) and then a Mexican free-tailed bat (*Tadarida brasiliensis*). The third attack, likely a big brown bat (*Eptesicus fuscus*) occurred after daylight. Later that night, he captured a hoary bat in a mist net that he thought was the same aggressive individual because of fresh blood on the animal's face and fur but no evidence of injury. He held it overnight; the following morning it was dead. It tested positive for rabies. These observations, with reports of aggression in captive rabid big brown bats [16,17], demonstrated that although aggressive behavior occurred in rabid bats, field observations of this behavior are relatively uncommon. Other reports of intra- and inter-specific aggression among free-ranging bats have been published, but the bats in those studies were not tested for rabies so the cause of the interactions remained unknown [22–25]. For example, mid-air and bat-to-bat attacks involving hoary bats, silver-haired bats, and tricolored bats (*Perimyotis subflavus*) have been interpreted as either aggression or predation attempts, but rabies infection was not confirmed [22,25]. Although some bat species prey on other bats or invertebrates, even during flight, documented cases of cannibalism among bats appears to be uncommon [26,27]. Thus, the observations of aggressive or predatory interactions alone cannot confirm whether rabies contributed to the behavior, emphasizing the value of laboratory confirmation when observing unusual interactions involving bats.

The rabies virus variant may also influence clinical expression and infection outcome in bats. Davis et al. [28] demonstrated that clinical response of big brown bats differed following experimental infection with rabies virus variants associated with different bat species. Variation in clinical expression among infected bats can contribute to differences in behavior and disease progression, potentially affecting opportunities to observe interactions involving rabid individuals in the wild.

Direct observations of rabid bats interacting aggressively with other animals can provide information that cannot be obtained by passive surveillance alone [29]. Surveillance records generally document the detection of a virus in a host after capture, death, or exposure of another animal, but rarely provide information about the behavior immediately preceding potential transmission. Behavioral observations can therefore provide context for how infected animals encounter potential hosts, how long contact is maintained, and whether interactions occur within or outside roosts or other aggregation sites [6]. Such observations are particularly relevant for bats because many contacts occur during nocturnal flight and may be difficult to distinguish from territorial interactions, predation, or other forms of social behavior without direct observation and diagnostic confirmation [30].

Big brown bats are a widely distributed species, occurring throughout a wide variety of ecosystems and elevational gradients in much of North America (Figure 1) and extending to South America and the Caribbean [31,32]. They are a reservoir for rabies in the USA [29,33] and a major one in some regions [1]. Flagstaff, Arizona, and surrounding areas have experienced repeated rabies outbreaks involving carnivores and RABV variants associated with bats. Each outbreak was caused by independent introduction of the virus into carnivores (striped skunks [*Mephitis mephitis*], grey foxes [*Urocyon cinereoargenteus*]; [10,34]). While conducting field work in northern Arizona during summer 2009, we observed an aggressive encounter between two big brown bats. Here, we describe this

direct field observation of intraspecific aggression by a rabid male big brown bat. In addition, we consider the potential influence of seasonal aggregation and concentrated water resources on opportunities for regional rabies activity, transmission, and spillover dynamics.

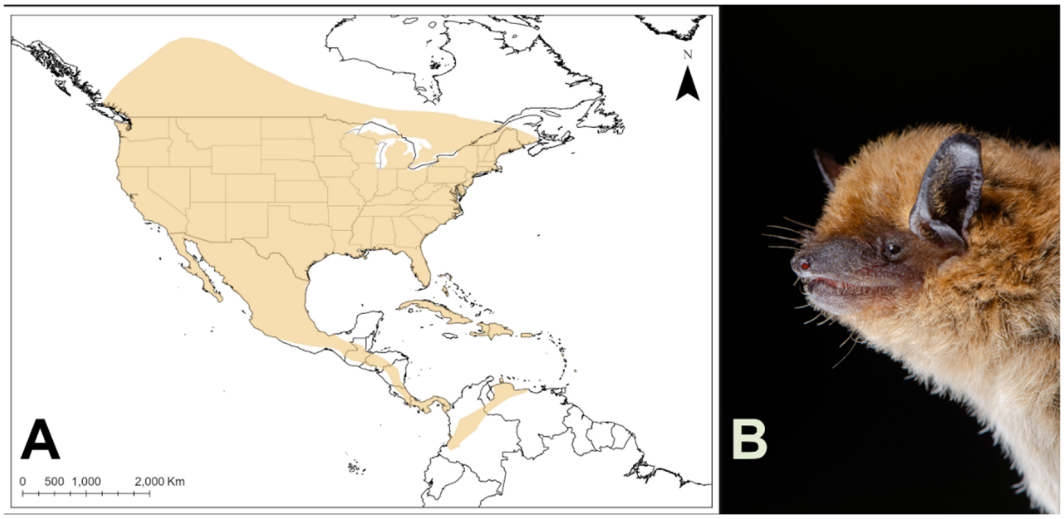

Figure 1. (**A**). Geographic range of the big brown bat (*Eptesicus fuscus*) which occurs from North America into the northern part of South America and is a known reservoir for rabies virus. (**B**). This species is commonly captured in northern Arizona (photo by J. G. Martínez-Fonseca).

2. Materials and Methods

On 30 June 2009, we set up mist nets to capture bats over a small water body (~30 × 30 m, 1 m deep; 35.882416°, −111.940258°, elevation 2150 m) in an area dominated by ponderosa pine (*Pinus ponderosa*) forest (Figure 2). Because water bodies occurred at low density in northern Arizona with (there were only 4 earthen ponds within the 6000 ha area centered on our capture site) and the nearest water sources were 2, 5, and 6 km away, these ponds typically received high use by bats during summer.

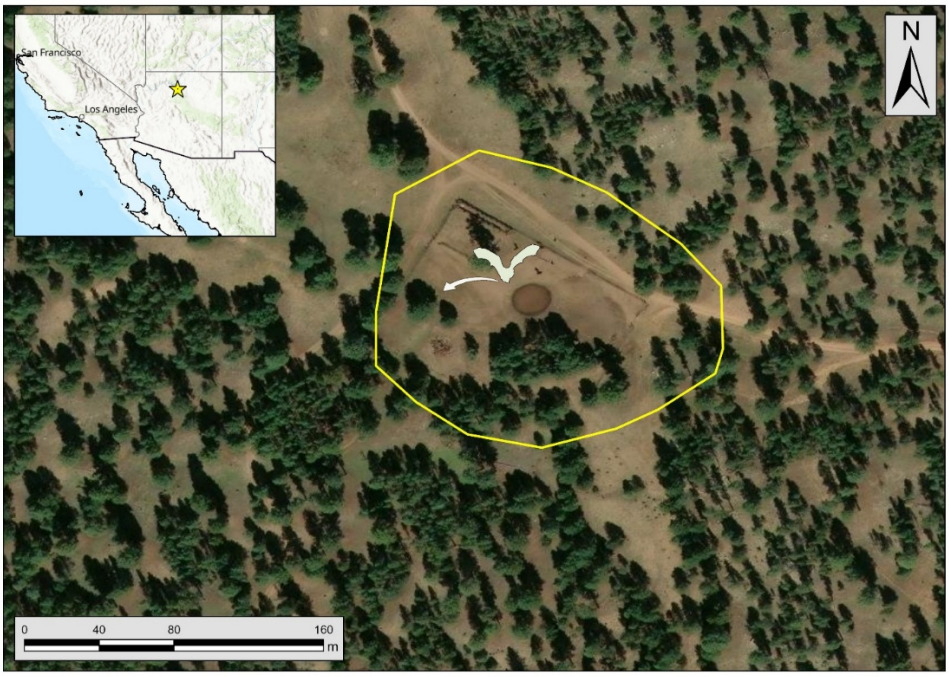

Figure 2. Location of a water body (within yellow circle) in ponderosa pine (*Pinus ponderosa*) forest of northern Arizona where a rabid big brown bat was observed attacking another big brown bat on 30 June 2009 (Google Earth imagery date: 7 June 2007). The white bat symbol depicts the original location of the aggressive big brown bat, which attacked another big brown bat at that site. The white arrow depicts the flight path of the two bats to a nearby ponderosa pine tree, from which they subsequently fell to the ground.

Concurrently, we were studying insectivorous bats in northern Arizona using live-capture techniques (mist netting) and genetic methods [35,36]. During the trapping period (20:30–23:30), the temperature decreased from 15 °C (when nets were opened) to 8.4 °C (when nets were closed), relative humidity increased from 45% to 65%; we received no precipitation. This was typical of the month; for a 19-year period, total precipitation for June averaged 1.5 cm and maximum and minimum temperatures averaged 26.9 and 8.7 °C, respectively [37]. In Arizona, a wet monsoon season typically begins in July, with the two previous months (June, July) the driest annually [38].

3. Results

After placement of nets, we typically waited until after civil twilight (20:15; sunset at 19:42) to open nets to avoid capturing birds. However, at 19:30, while still daylight, three members of our team observed a single male big brown bat flying in a zig-zag pattern west of the pond about 6 to 8 m above ground. The bat was vocalizing audibly, loudly enough to draw attention of the field crew members, which was unusual behavior for a bat. We watched this bat for several minutes, at which point another bat flew towards the pond. The first bat then pursued the second bat and attacked it in flight, with the aggressor intercepting and interrupting the flight path of the second bat. The aggressive bat continued to fly on its original flight path, which differed from the non-aggressor's flight path. It thus appeared as if the attacking bat was forcing the second bat towards a ponderosa pine tree ~25 m west of the pond. We also noted that the two bats appeared to be flying as if locked together. We followed the bats to the tree, observed them land in the tree ~4 m above ground, and within 30 s, fall from the tree to the ground. On the ground, we observed that the aggressive bat was maintaining a prolonged bite hold on the lower jaw of the non-aggressive bat; this appeared to have occurred during the entire encounter and was the reason why the bats seemed to be joined together when in flight. As the bats lay on the ground, we were able to visually confirm identification of both individuals as big brown bats. Within 30 s, the aggressive bat released the non-aggressive individual, and the non-aggressor then flew off and could not be further observed. However, the aggressor, a reproductive male, remained on the ground while we obtained equipment to hold and examine the bat. The interaction was observed continuously by field crew members from the initial pursuit until the bats fell to the ground. Observers followed the bats visually from the pond to the tree and approached the animals on the ground to confirm species identification. Because of this bat's unusual behavior and inability to fly, we euthanized it using isoflurane and cervical dislocation. Brain tissue from the bat was submitted to the Arizona Department of Health Services State Laboratory and tested for rabies virus antigen using the direct fluorescent antibody (dFA) test following standard Centers for Disease Control and Prevention protocols [39]. The bat subsequently tested positive for rabies; however, viral variant typing was not performed.

During the evening, we captured 156 bats representing at least nine species (Table 1). Two species, California myotis (*Myotis californicus*) and western small footed myotis (*Myotis ciliolabrum*), were difficult to distinguish morphologically so were combined (Table 1). The remaining captures comprised seven additional taxa representing two families (Vespertilionidae and Molossidae). Thus, the observation occurred at a site supporting a multispecies assemblage rather than an aggregation composed exclusively of big brown bats. In addition, some of these species (e.g., Mexican free-tailed bat, hoary bat) have the capability of long distance flight. Although 61% of bats captured were female, most females were big brown bats and almost half of all females were reproductive (pregnant or lactating; Table 1).

Table 1. Bats captured on 30 June 2009 between 20:30 and 23:30 at an earthen pond in northern Arizona by sex and reproductive status (R = reproductive [Females: pregnant or lactating; Males: testes descended], N = non-reproductive, U = unknown).

		Female			Male			Total
Species	**Common name**	**R**	**N**	**U**	**R**	**N**	**U**	
Antrozous pallidus	Pallid bat	2	0	0	0	0	0	2
Corynorhinus townsendii	Townsend's big-eared bat	1	0	0	0	0	0	1
Eptesicus fuscus	Big brown bat	59	10	2	10	13	1	95
Lasiurus cinereus	Hoary bat	0	0	0	3	9	0	12
Lasionycteris noctivagans	Silver-haired bat	0	0	0	0	0	1	1
Myotis californicus / ciliolabrum	California or western small-footed myotis	1	1	2	2	3	1	10
Myotis thysanodes	Fringed myotis	2	0	0	2	0	0	4
Myotis volans	Long-legged myotis	6	2	1	1	9	1	20
Tadarida brasiliensis	Mexican free-tailed bat	1	4	1	0	4	1	11
Total		72	17	6	18	38	5	156

Big brown bats represented 61% of our captures; we captured more females (n = 71 females [59 reproductive: 23 pregnant and 36 lactating]) than males (n = 24, 13 with enlarged scrota). A large snag (>60 cm of diameter at breast height), 12 m north of the pond, could have served as a maternity roost and we observed other snags in close proximity to the site that could be roost structures [40,41]. This capture rate was typical of other nights that we netted bats at this site (Table 2); number captured per night averaged 152 ± 26 bats (range 61 to 235). Percentage of big brown bats captured at this site was consistently high, ranging from 26 to 71%, and capture rate ranged from 2 to 9 animals per net hour (Table 2). The lowest number of captures (n = 61) with lowest percentage of big brown bats occurred in August, when the monsoon season increased rainfall and available moisture in northern Arizona [37,38]; however, the capture rate was still comparable to other dates. The warm, dry period in June and July prior to monsoon season and proximity to potential roost(s) likely led to high numbers of bats aggregating at this site.

Table 2. Captures of bats at a pond in northern Arizona where an aggressive big brown bat (*Eptesicus fuscus*) was observed on 30 June 2009. The bat subsequently tested positive for rabies. Number of net hours is the number of 6-m nets opened for 1 h during a netting session. Netting sessions usually started ~20:15 and ended between 23:00 and 01:00.

Date	Number of Net Hours	Number of Bats	Capture Rate of Bats (# per net h)	Number of Big Brown Bats	Percentage of Big Brown Bats (%)	Capture Rate of Big Brown Bats (# per net h)
28 June 2007	32	235	7	89	38	3
19 July 2007	23	208	9	120	58	5
23 July 2008	54	100	2	59	59	1
30 June 2009	42	156	4	95	61	2
11 August 2009	21	61	3	16	26	1
23 June 2011	36	152	4	108	71	3

4. Discussion

Rabies can produce a range of neurological and behavioral expressions in bats with clinical presentation varying among individuals, host species, and viral variants. Frequently, rabid bats exhibit neurological impairment manifested as lethargy, social withdrawal, abnormal activity such as daytime flight, or motor impairment resulting in an inability to fly [1,3,19,42]. In particular, the encephalitic (furious) form of rabies can involve behavioral excitation, altered responsiveness, vocalization, aggression, and biting [3,43]. Our observation provides an example of this behavioral component of rabies in a free-ranging big brown bat. The attacking bat demonstrated several behaviors consistent with rabies including audible vocalization, erratic flight, daytime activity, pursuit of another bat, and prolonged biting. These behaviors occurred in an animal subsequently confirmed to be infected with RABV, although our observation could not establish that each behavior was caused by rabies. Similar aggressive behavior was described in rabid big brown bats in captivity [16,17] and in free-ranging bats [20,21]. Because bats are nocturnal, highly mobile, and difficult to observe continuously, direct observations of interactions under free-ranging conditions such as these are likely limited and thus underreported. Rather than indicating that aggression is an unusual manifestation of rabies, the limited number of detailed field observations may reflect the difficulty of detecting and documenting brief interactions and suggests that behavioral variation (e.g., aggressive interactions) among infected bats should be considered when evaluating potential mechanisms of RABV transmission. This behavioral variability may be particularly relevant when interpreting field observations of potential transmission events and may justify inclusion in models of bat rabies transmission.

The incident we observed occurred during the maternity period rather than during the time associated with autumn mating and increased male reproductive activity (August–October), making it unlikely that aggression was related to reproductive or competitive behavior. During the evening that we documented the event, we did capture adult male big brown bats with descended testes, so territorial behavior could not be completely excluded as a contributing factor. However, big brown bats have a dissociated pattern of reproduction with mating asynchronous from development of sex hormones [44]. In addition, adult males (although less abundant) can occur at maternity roosts due to natal philopatry (i.e., inexperienced young males born the previous year return to natal sites). They might also choose to conserve energy at colder higher elevations through heterothermy (i.e., males roosting independently from maternity colonies) and since they have no need to tend young as do females, are able to achieve lower body temperatures for energetic savings [45]. The event did coincide with the peak parturition and lactation period, which for big brown bats, occurs from June through early July [46,47]. During this period, female big brown bats may aggregate in maternity colonies numbering hundreds of individuals ([1,48], C. L. Chambers, unpublished data) and the predominance of female big brown bats captured during our sampling suggested that maternity colonies were close to our water source. Concentrations of big brown bat females, males, and other bats within a relatively small area could increase the frequency with which individuals encounter each other,

particularly when bats leave or return to roosts or converge on predictable resources for drinking or foraging (e.g., social foraging; [49,50]). Aggregation does not imply that all contacts are aggressive, but increased contact rates could increase opportunities for potentially infectious contacts to occur and transmit disease. Seasonal variation in rabies dynamics may thus be partly influenced by host reproductive ecology.

The aggressive big brown bat displayed several behaviors that could be associated with rabies, including daylight activity, erratic flight, and audible vocalization. The prolonged bite observed in this incident is relevant to rabies transmission because RABV is transmitted primarily through virus-containing saliva introduced into tissue, most commonly through a bite [6]. The attacking bat maintained contact with the lower jaw of the other bat rather than biting briefly and immediately disengaging. Prolonged attachment could increase the duration of exposure of a bite wound to saliva, although we did not determine whether the second bat sustained a wound or became infected. Thus, the observation documents a behavior that is compatible with the established mechanism of RABV transmission but did not demonstrate transmission. This distinction is important because infection status was not determined for the second bat and the interaction was not followed after the animal flew away. Experimental work in captive big brown bats also failed to detect bat-to-bat transmission despite limited viral excretion in saliva [18], illustrating that the occurrence of a bite does not necessarily result in transmission. Nevertheless, biting by a rabies-infected animal of a conspecific or another animal can be an effective mechanism for successful viral transmission. This behavior has been described in many mammals, especially in those with clinical symptoms of rabies, including rabid big brown bats [16,17,21], providing useful behavioral information about how opportunities for exposure may arise in naturally infected bats.

An alternative interpretation of an aggressive interaction between bats is predation or opportunistic feeding. Several bat species are capable of attacking and consuming other vertebrates, and predatory interactions can occur during flight [27,51]. Consequently, aggression observed in a free-ranging bat cannot necessarily be attributed to rabies without additional evidence. In our case, several factors distinguished the observation from a predatory event. The interacting bats were identified as conspecific big brown bats, the second bats subsequently flew away, and the attacking bat remained grounded and exhibited other abnormal behaviors and was later confirmed to be rabies positive. These observations are consistent with an association between the encounter and rabies infection but do not establish that rabies caused the attack or exclude other contributing factors.

Water availability may have been particularly important in creating the circumstances for this encounter. The observation occurred during late June in an arid environment in northern Arizona, before the onset of the summer monsoon season, when surface water can be spatially restricted across otherwise dry landscapes [38,52]. Bats commuting from roosts or foraging areas may therefore converge repeatedly and frequently on relatively few dependable water sources. We noted high capture rates of bats and bat species at this site, supporting the importance of water during the dry season as an aggregation point. Although capture rates do not provide a direct measure of contact rates, the concentration of many bats at a single water source indicated that the site functioned as an important resource for bats in the surrounding landscape (e.g., [53]).

Concentrated resources can increase opportunities for contact among individuals by bring bats to the same location repeatedly. At water sources, bats may encounter others when approaching, circling, drinking, foraging, or departing from the resource. These encounters may range from brief contacts to prolonged interactions, such as biting, that provide opportunities for RABV transmission. The presence of multiple species also creates opportunities for interspecific encounters. Capture rates and the consistently high proportion of big brown bats at our site support the importance of this water source as an aggregation point. Resource-associated aggregation has been identified as a potential contributor to bat contact and spillover dynamics in northern Arizona [53,54]. Although we did not directly observe other mammals congregating at this stie, terrestrial vertebrates may encounter and scavenge infected bats or carcasses associated with water sources and nearby roosts, providing additional opportunities for RABV exposure [53,54]. These interactions may become particularly important during dry years when fewer water sources are available and bats become concentrated at remaining reliable resources. Resource-driven aggregation can therefore increase opportunities for interactions among bats, as well as between bats and terrestrial vertebrates, creating opportunities for RABV transmission and spillover. This possibility is relevant in northern Arizona, where repeated rabies outbreaks involving bats and mesocarnivores was documented in the Flagstaff area [34], approximately 85 km from our study site. Water resources and nearby roosts can function as focal points where interactions among bats, as well as between bats and terrestrial vertebrates, create opportunities for RABV transmission and spillover. Rabies transmission opportunities may therefore be enhanced by resource-driven aggregation around limited water availability in arid environments.

Several limitations should be considered regarding this observation. First, only the attacking bat was recovered and tested, preventing confirmation of infection status of the second individual or transmission outcome since it flew away. Second, although the attacking bat exhibited several behaviors consistent with neurological

disease, we cannot determine which were directly caused by rabies. The fall from the tree may also have contributed to the individual's subsequent inability to fly, although the bat displayed abnormal behavior before the fall. Third, the observation was opportunistic and provided no estimate of the frequency of aggressive interactions among rabid bats. This event should therefore not be interpreted as evidence that aggressive interactions are common or that water-source aggregation necessarily increases RABV transmission. Finally, we did not characterize the viral variant infecting the bat, which limits our inference about whether the behavioral expression we observed might have been associated with a particular RABV variant. These limitations emphasize that the primary contribution of this observation is behavioral documentation rather than demonstration of transmission.

Our observation of this incident documents aggressive behavior and prolonged biting by a free-ranging big brown bat subsequently confirmed to be infected with rabies. The encounter occurred during the maternity period at a water source supporting a multi-species bat assemblage, providing context in which contact among bats may be concentrated. Although we cannot demonstrate that rabies caused the aggression or resulted in transmission to the second bat, the observation highlights the interaction between seasonal host ecology (reproduction, aggregation) and environmental limitations (water, climate) that may influence rabies transmission dynamics. Continuing to document events such as this, with diagnostic confirmation and information on host behavior and resource use, can improve our understanding of the behavioral pathways through which RABV is maintained and transmitted among bats and potentially spilled over to other mammals, suggesting that behavioral variability should be considered in future studies and models of bat rabies transmission and spillover ecology.

Author Contributions

C.L.C.: conceptualization, methodology, investigation, writing—original draft, project administration; J.G.M.-F.: visualization, writing—review and editing; D.L.B.: conceptualization, methodology, writing—review and editing. All authors have read and agreed to the published version of the manuscript.

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Informed Consent Statement

Not applicable.

Data Availability Statement

All relevant data is presented in the main body of this manuscript.

Conflicts of Interest

The authors declare no conflict of interest.

Use of AI and AI-Assisted Technologies

No AI tools were utilized for this paper.

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