Bovicola tibialis (Phthiraptera: Trichodectidae): Occurrence of an Exotic Chewing Louse on Cervids in North America

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ABSTRACT Through a recent (2003–2007) survey of ectoparasites on hoofed mammals in western North America, a literature review, and examination of archived museum specimens, we found that the exotic deer-chewing louse, *Bovicola tibialis* (Piaget), is a long-term, widespread resident in the region. The earliest known collection was from Salt Spring Island, Canada, in 1941. We found these lice on the typical host, that is, introduced European fallow deer (*Dama dama* L.), and on Asian chital (*Axis axis* [Erxleben]), native Columbian black-tailed deer (*Odocoileus hemionus columbianus* [Richardson]), and Rocky Mountain mule deer (*O. h. hemionus* [Rafinesque]) × black-tailed deer hybrids. Chital and the hybrid deer are new host records. All identified hosts were known to be or probably were exposed to fallow deer. Geographic records include southwestern British Columbia, Canada; Marin and Mendocino Counties, California; Deschutes, Lincoln, and Linn Counties, Oregon; Yakima and Kittitas Counties, Washington; Curry County, New Mexico; and circumstantially, at least, Kerr County, Texas. All but the Canadian and Mendocino County records are new. *Bovicola tibialis* displays a number of noteworthy similarities to another exotic deer-chewing louse already established in the region, that is, *Damalinia* (*Cervicola*) sp., which is associated with a severe hair-loss syndrome in black-tailed deer. We discuss longstanding problems with proper identification of *B. tibialis*, the probability that it occurs even more widely in the United States, and the prospects for it to cause health problems for North American deer. Additional information gathered since our active survey establishes further new distribution and host records for *B. tibialis*.

KEY WORDS hair loss, exotic pediculosis of deer, EPOD, *Dama dama*, *Odocoileus hemionus*

During a recent survey for exotic Asian chewing lice known to be associated with a pathologic hair-loss syndrome (HLS) in native deer in the North American Pacific Northwest, we unexpectedly encountered the widespread presence of *Bovicola tibialis* (Piaget) (Phthiraptera: Trichodectidae), a European chewing louse parasite of fallow deer, *Dama dama* L. Some infestations by *B. tibialis* now seem to be causing deer-host hair loss much like that previously associated with the Asian lice.

In the mid-1990s, native populations of the Columbian black-tailed deer, *Odocoileus hemionus columbianus* (Richardson) (BTD), began to display signs of mysterious and unprecedented hair loss. The syndrome is characterized by a general decline in body condition and a loss of pelage, especially over the thorax, flanks, and hindquarters. The most severe cases may progress to morbidity and mortality. Victims are mostly young deer, especially does, and the syndrome is most evident in the winter and spring. HLS was noted first by wildlife biologists in Washington (Foreyt et al. 2004), but deer showing similar signs soon appeared in Oregon, as well (Bildfell et al. 2004).

The etiology of HLS is not well understood and may depend on the convergence of several predisposing factors (Bender and Hall 2004, Bildfell et al. 2004). However, one consistent and possibly critical element is the presence on affected animals of large populations of chewing lice (Phthiraptera: Ischnocera: Trichodectidae). The lice in question were an undetermined species of *Damalinia* (*Cervicola*), a subgenus of artiodactyl parasites whose only known members are endemic to the Eastern Hemisphere. It follows, then, that the lice are introduced exotics whose normal hosts are some Old World artiodactyl, probably a cervid, and BTD are aberrant, but acceptable hosts. Such colonizations of local vertebrate hosts by exotic parasites are prone to pathological outcomes (Brunetti and Cribbs 1971, Foreyt et al. 1986, Hoberg et al. 2001), and we believe that naive, young, and winter-

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stressed BTD are particularly susceptible to attacks by this *Cervicola* louse. Exploding populations of the lice are extremely irritating to the host victims, leading them to excessive grooming behavior that only exacerbates extensive pelage damage already exacted by feeding activities of huge numbers of lice (Bildfell et al. 2004).

In an effort to assess the geographic extent, chronological progression, and host specificity of HLS and *Cervicola* sp. infestations, we extensively surveyed and examined a variety of native and exotic artiodactyl species for ectoparasites along the West Coast of North America between 2003 and 2007. Incidental to this effort, we encountered several other unusual parasites, including the unexpected presence in several localities of another exotic cervid-chewing louse, *B. tibialis,* a specific parasite of the European fallow deer. In this study, we present information gathered on the occurrence of *B. tibialis* in North America and pathology circumstantially associated with its presence on native deer.

Materials and Methods

Between March 2003 and September 2007, we acquired, examined, and identified ≈500 collections of ectoparasites from various free-ranging and captive artiodactyls in California, Oregon, Washington, and British Columbia, Canada. Most of the host animals were BTD, but variable sample numbers came from mule deer (*O. h. hemionus* [Rafinesque], MD), BTD × MD hybrid animals, Columbian white-tailed deer (*Odocoileus virginianus leucurus* [Douglas]), Northwest white-tailed deer (*O. virginianus ochrourus* V. Bailey), Roosevelt elk (*Cervus canadensis roosevelti* Merriam), sika deer (*C. nippon* Temminck, sensu lato), fallow deer, and chital (*Axis axis* [Erxleben]). A few examined samples came from captive aoudad (*Ammotragus lervia* [Pallas]), greater kudu (*Tragelaphus strepsiceros* [Pallas]), and slender-horned gazelle (*Gazella leptoceros* Cuvier). Many of the parasite samples were collected from targeted wild animals showing signs of HLS and killed (or anesthetized) by wildlife biologists for surveillance examination. Others were collected during necropsies of animals opportunistically found dead from road accidents or natural causes; from hunter-killed animals at check stations; or from captive/farmed animals harvested for commercial purposes, dead of natural causes, or anesthetized for examination.

Most of the parasites were found by visual examination of the host pelage, collected by hand, mostly using fingers or forceps, and preserved in 70–95% alcohol (ethyl or isopropyl). A few collections were made from fresh or frozen hides of harvested hosts by soaking and digesting the hides/pelage in 10% aqueous sodium hydroxide, filtering the resulting liquid through no. 90 cheesecloth, hand sorting the parasites from the residue using a fluorescent-lit 3× magnifying lens, and transference to alcohol preservative. In addition to these purposeful contemporary samples, we acquired and examined small numbers of pertinent slide-mounted archival specimens of cervid-chewing lice with regional origins from entomological collections at the Spencer Entomological Collection (University of British Columbia, Vancouver, BC, Canada) and the United States National Parasite Collection (USNPC, United States Department of Agriculture [USDA], Agricultural Research Service, Beltsville, MD).

Parasite identifications were done at the USDA, National Veterinary Services Laboratories (NVSL, Ames, IA). The great majority were made under a dissecting microscope at magnifications up to ×60 by J.W.M. using standard taxonomic reference guides. The small number of borrowed slide-mounted louse specimens was studied and identified under a compound microscope using differential interference contrast illumination at magnifications up to ×400. The basic references for chewing louse identifications were Lyal (1985), Werneck (1950), and Price et al. (2003), supplemented by original descriptions, other descriptive literature, and reference specimens in the NVSL parasitology collection. For verification of subject louse species identification, we borrowed and studied voucher samples of *B. tibialis* collected on free-ranging fallow deer in Europe from the entomology collection at the Natural History Museum (London, United Kingdom). We follow the supraspecific louse taxonomy proposed by Lyal (1985) and the taxonomy of Pitra et al. (2004) and Groves (2005) for cervids.

For perspective and completeness, we reviewed, evaluated for validity, and summarized previously published citations mentioning the existence of exotic lice on cervid hosts in North America.

Representative vouchers of studied lice are retained in the NVSL parasitology reference collection, or at other listed institutions, with accession numbers as given in the text and in Table 1.

Results

The general groups of ectoparasites collected from the examined hosts comprised ticks (Acari: Ixodidae), chiggers (Acari: Trombiculidae), keds (Diptera: Hippoboscidae), fleas (Siphonaptera: Pulicidae), sucking lice (Phthiraptera: Linognathidae), and chewing lice (Phthiraptera: Trichodectidae). We found among them a number of interesting parasite records and host relationships that will be detailed elsewhere, but in this study we present evidence we found that is pertinent only to the widespread existence of a European chewing louse, *B. tibialis,* on cervid hosts in North America.

Table 1 details the valid records (through 2007) for collections of *B. tibialis* in North America. Our contemporary surveillance efforts found two previously unknown foci of infestation in California and Washington, respectively, and infested captive hosts in three Oregon sites. Our retrospective study of borrowed archival louse specimens revealed several other infested sites in British Columbia, Canada, and New Mexico, some of which are previously documented

Table 1. Valid North American collection records for *Bovicola tibialis* on cervid hosts

Collection date	Locality	Collector	Host[a]	Repository/no.	Counts and comments
2 Feb. 1941	Salt Spring Island, British Columbia, Canada	I. McT. Cowan	*Odocoileus hemionus columbianus*	UBC[b]	2 ♀, 6 N (previously misidentified as *Tricholipeurus sp.*)
Dec. 1948	Campbell River, Vancouver Island, British Columbia, Canada	G. L. Spencer	*Odocoileus hemionus columbianus*	UBC	1 ♀ (previously misidentified as *Tricholipeurus lipeuroides*)
5 Feb. 1954	Vancouver, British Columbia, Canada	G. L. Spencer	*Odocoileus hemionus columbianus* (captive)	UBC	1 ♀ (previously misidentified as *Tricholipeurus lipeuroides*)
8 Feb. 1954	Vancouver, British Columbia, Canada	G. L. Spencer	*Odocoileus hemionus columbianus* (captive)	UBC	2 ♀, 6 N (previously misidentified as *Tricholipeurus sp.*)
31 Jan. 1973	Hopland Research & Extension Center, Mendocino Co., CA	D. R. Westrom	*Odocoileus hemionus columbianus* (captive)	NHM[c]	2 ♀ (up to 8,200 lice seen per animal)
23 Dec. 1983	Hillcrest Park Zoo, Clovis (Curry Co.), NM	G. S. Pfaffenberger	*Axis axis* (captive)	USNPC[d] 078178.01	2 ♀ (previously misidentified as *Damalinia* [*Cervicola*] *forficula*)
9 Nov. 2004	Troyer Deer Farm, Lincoln Co., OR	J. Mortenson	*Dama dama* (farmed)	NVSL[e] 442614	2 ♀ (bulk digestion of 8 frozen hides)
21 Dec. 2004	Throop Deer Farm, Linn Co., OR	J. Mortenson	*Dama dama* (farmed)	NVSL 442616	1 ♀ (bulk digestion of 9 frozen hides)
21 Dec. 2004	Throop Deer Farm, Linn Co., OR	J. Mortenson	*Dama dama* (farmed)	NVSL 442617	87 ♀, 2 N (bulk digestion of 9 frozen hides)
21 Dec. 2004	Throop Deer Farm, Linn Co., OR	J. Mortenson	*Dama dama* (farmed)	NVSL 392659	10 ♀ (single hide digestion)
21 Dec. 2004	Throop Deer Farm, Linn Co., OR	J. Mortenson	*Dama dama* (farmed)	NVSL 392661	14 ♀ (single hide digestion)
21 Dec. 2004	Throop Deer Farm, Linn Co., OR	J. Mortenson	*Dama dama* (farmed)	NVSL 396262	11 ♀ (single hide digestion)
21 Dec. 2004	Throop Deer Farm, Linn Co., OR	J. Mortenson	*Dama dama* (farmed)	NVSL 400303	38 ♀ (single hide digestion)
21 Dec. 2004	Throop Deer Farm, Linn Co., OR	J. Mortenson	*Dama dama* (farmed)	NVSL 400304	17 ♀, 2 N (single hide digestion)
24 Jan. 2005	Game Management Unit 346, Yakima Co., WA	B. Hall	*Odocoileus h. hemionus* × *columbianus*	NVSL 366070	17 ♀, 1 N
29 Mar. 2005	Game Management Unit 346, Yakima Co., WA	B. Hall	*Odocoileus h. hemionus* × *columbianus*	NVSL 370466	11 ♀
29 Mar. 2005	Game Management Unit 346, Yakima Co., WA	B. Hall	*Odocoileus h. hemionus* × *columbianus*	NVSL 370468	22 ♀
29 Mar. 2005	Game Management Unit 346, Yakima Co., WA	B. Hall	*Odocoileus h. hemionus* × *columbianus*	NVSL 370469	19 ♀
29 Mar. 2005	Game Management Unit 346, Yakima Co., WA	B. Hall	*Odocoileus h. hemionus* × *columbianus*	NVSL 370470	2 ♀
22 Apr. 2005	Point Reyes National Seashore, Marin Co., CA	J. Mortenson	*Dama dama* (feral)	NVSL 374315	1 ♀ (on 1 of 11 individually digested hides)
1 Nov. 2005	Troyer Deer Farm, Lincoln Co., OR	J. Mortenson	*Dama dama* (farmed deer)	NVSL 409190	2 ♀ (single hide digestion)
15 Nov. 2005	Troyer Deer Farm, Lincoln Co., OR	J. Mortenson	*Dama dama* (farmed deer)	NVSL 414629	4 ♀ (single hide digestion)
15 Nov. 2005	Troyer Deer Farm, Lincoln Co., OR	J. Mortenson	*Dama dama* (farmed deer)	NVSL 414637	1 ♀ (single hide digestion)
30 Dec. 2005	Pederson Deer Farm, Deschutes Co., OR	J. Mortenson	*Dama dama* (farmed deer)	NVSL 417396	1 ♀ (bulk digestion of 3 frozen hides)
16 Mar. 2006	Game Management Unit 346, Yakima Co., WA	J. Bernatowicz	*Odocoileus h. hemionus* × *columbianus*	NVSL 433881	21 ♀, 1 N
17 Mar. 2006	Game Management Unit 346, Kittitas Co., WA	J. Bernatowicz	*Odocoileus h. hemionus* × *columbianus*	NVSL 433641	88 ♀, 36 N, 1 nit
17 Mar. 2006	Game Management Unit 346, Kittitas Co., WA	J. Bernatowicz	*Odocoileus h. hemionus* × *columbianus*	NVSL 433879	29 ♀, 4 N
20 Mar. 2006	Game Management Unit 346, Kittitas Co., WA	J. Bernatowicz	*Odocoileus h. hemionus* × *columbianus*	NVSL 433885	37 ♀, 1 N

[a] Free-ranging wildlife unless otherwise noted.
[b] University of British Columbia, Spencer Entomological Museum, Vancouver, BC, Canada.
[c] Natural History Museum, London, United Kingdom.
[d] United States National Parasite Collection, Agricultural Research Service, United States Department of Agriculture, Beltsville, MD.
[e] National Veterinary Service Laboratories, Animal and Plant Health Inspection Service, United States Department of Agriculture, Ames, IA.

(Bildfell et al. 2004). Our literature review found one additional, valid, historical record for *B. tibialis* in California (Westrom et al. 1976).

The earliest extant collection of *B. tibialis* in North America was made in 1941 on Salt Spring Island in British Columbia, Canada (Table 1). Other archival specimens in the University of British Columbia's Spencer Entomological Collection demonstrate that the louse was present also on nearby Vancouver Island, and possibly on the mainland, as well, through 1954. As two of us (J.W.M. and J.A.M.) have previously discovered and disclosed (Bildfell et al. 2004), all of these specimens were taken from native BTD and misidentified as endemic species of chewing lice (Cowan 1946, Hopkins 1960). The source of these exotic lice is undoubtedly cross-contamination from European fallow deer introduced and established at these sites in the 1930s (Nagorsen 1990, Shackleton 1999).

A number of other North American records for *B. tibialis* are previously published, but we believe that only one of them (Westrom et al. 1976) is legitimate. BTD again were the hosts in this case, and again, these captive animals were subject to close contact with cohabiting fallow deer as an obvious source of louse infestation. Although Westrom (personal communication) currently possesses no voucher specimens from his studies, we serendipitously located, borrowed, and studied two such lice (Table 1) from the collection at the British Natural History Museum. They are identical to the lice in all our other collections from endemic North American deer and to specimens of European origin.

Other published North American records for *B. tibialis* (Kellogg 1908, Kellogg and Ferris 1915, Bucknell 1934, Whitlock 1939, Longhurst and Douglas 1953, Taber and Dasmann 1958, Browning and Laupe 1964) are less certain. Nothing in the circumstances of any of these reports suggests that the lice encountered were, in fact, *B. tibialis*, with one curious exception. Longhurst and Douglas (1953) studied interrelationships of parasites of domestic sheep, *Ovis aries* L., and BTD at the University of California Hopland Field Station (Mendocino County; now known as the Hopland Research and Extension Center) that was the same locality – evidently by pure coincidence – where Westrom et al. (1976) found *B. tibialis* >20 yr later. Chewing lice on BTD in the 1950s study were putatively *B. tibialis*, as well, but fallow deer (one male and one female) were not introduced to the field station until 1965 (Westrom et al. 1976), and without an evident source for the earlier alleged *B. tibialis*, that louse identification must surely be erroneous. All of the other questionable early records of the louse in North America cite native *Odocoileus* deer as the hosts, and none of them mentions any connection to fallow deer. Moreover, Hopkins (1960), Walker and Becklund (1970), and Westrom et al. (1976) all discount the earlier reports of *B. tibialis* in North America as louse misidentifications tied back to an erroneous, but persistent referral by Osborn (1896). We agree.

Our examination of museum-held louse specimens from western deer yielded one additional and anomalous record for *B. tibialis.* Two females were collected in 1983 at a zoo in Clovis (Curry County), New Mexico (Table 1). These lice are on a microscope slide at the USNPC and were misidentified as *Damalinia* (*Cervicola*) *forficula* (Piaget). At the present late date, we are unable to independently verify any of the other collecting data on the label of the slide or in the records of its USNPC repository. The putative host was a captive chital, which would have been an expected host for *D. forficula,* probably explaining the initial louse misidentification. Perhaps the host was misidentified, as well, and was, in fact, a fallow deer. The more likely scenario, however, is that the host was a chital that was housed together with captive fallow deer, allowing for ectoparasite cross-contamination. Although chital are no longer present at the Hillcrest Park Zoo, according to the curator (M. Yannotti, personal communication), the facility does currently own fallow deer and has shown them periodically over the last 30 yr. The same Texas animal dealer historically supplied both deer species to the zoo, and both were probably present and housed together in 1983. In any case, the locality record for the collection seems to be valid, and if the host identification is accurate, this would be a new host record, as well. The single collection of possibly stray lice on this host is of dubious importance, however.

The remaining records for *B. tibialis* in Table 1 all were incidental results from our extensive recent survey for *Damalinia* (*Cervicola*) lice on western deer. All of the Oregon records are from captive fallow deer held on three separate deer farms in three different counties. The lice from Lincoln County, Oregon, in November 2004 are actually the first documented specimens of *B. tibialis* on its typical host in North America. We note with no evident explanation that the average body size of studied *B. tibialis* specimens from North American fallow deer hosts is slightly smaller than that for studied specimens from both European fallow deer and native *Odocoileus* deer hosts.

The single louse (Table 1) from Marin County, California, was the only specimen found in the examination of digested hides from 11 free-ranging fallow deer. Evidently, fallow deer sustain only small populations of lice at this site, at least in the spring. The opportunity to examine these animals resulted from an effort by the USNPS to extirpate free-range populations of exotic chital and fallow deer that have existed on federal land at the Point Reyes National Seashore since their introduction for hunting in the 1940s. The original stock of 28 *D. dama* came from the San Francisco Zoo (Long 2003, USNPS 2006), and the presence of *B. tibialis* on these fallow deer at this site probably traces its origins filially to the introduction of those hosts. The herd at Point Reyes recently numbered ≈860 animals (Fellers and Osbourn 2007), but more recent extirpation activities have decimated the local population.

Our discovery of *B. tibialis* on hybrid BTD × MD in Yakima and Kittitas Counties, Washington, was comparatively unexpected. Both subspecies of *O. hemionus* occur naturally in this area and interbreed to some extent. The host animals were wild native deer. The 2005 collections were from animals that a local resident has been recreationally feeding for several years. The resident noticed that some of the deer were looking scruffy and requested a herd health check. Lice later identified as *B. tibialis* were found on selected animals anesthetized for examination, and condition of the pelage of these deer seemed to correlate inversely with the numbers of lice present on each examined host. The follow-up collections in the same area in 2006 were more directed at assessing the lice and were from wild deer on normal winter range. We could find no fallow deer in the area at present, but interviews with local residents and wildlife people provided anecdotal evidence that captive fallow deer existed there during the 1980s, with frequent escapes. Witmer and Lewis (2001) stated that a small, localized population of free-ranging fallow deer existed in nearby King County since the early 1980s.

Discussion

Widespread occurrence of exotic *B. tibialis* lice in North America is not particularly surprising. The story goes that George Washington brought the first fallow deer to the United States for his Mt. Vernon, Virginia, estate (Mungall and Sheffield 1994); their typical lice probably came with them, as well, even though these parasites since have gone largely unreported in North America. Our demonstration of the presence of *B. tibialis* at several western North American localities partially fulfills a prediction by Durden (2001) that this species and several other exotic lice probably occur here as a result of the introduction of their typical hosts. Surprisingly, nobody else has since taken up the challenge to provide evidence in support of that prediction. Although many of our survey records of *B. tibialis* are from hosts other than fallow deer, all of them are from animals actually or plausibly exposed to introduced *D. dama.*

Fallow deer are among the most widely introduced ungulates worldwide (Chapman and Chapman 1980), and it seems likely that *B. tibialis* is almost as well traveled. The prehistoric geographic range of *D. dama* probably covered much of Europe, but by the last Ice Age, they were nearly extinct in their native lands (Chapman and Chapman 1975, 1980; Chapman 1993; Long 2003). Human intervention and redistribution beginning in Roman times and continuing through the Middle Ages eventually reversed the decline, and this species once again is common across Europe.

Long (2003) details numerous North American introductions of fallow deer, but the current status of most of them is in doubt. Established free-ranging populations seem to persist in at least five states in the eastern United States, that is, Alabama, Georgia, Illinois, and Kentucky/Tennessee (Gray 1983, Whitaker 1996, Whitaker and Hamilton 1998, Long 2003, USDA 2008). The herd of white fallow deer at the United States Department of Energy, Argonne National Laboratory site (DuPage County, IL), is the least publicized of these populations. It sometimes burgeons to >400 animals, but usually comprises ≈40 (Gray 1983, Argonne National Laboratory 2008). It originated in ≈1940 from two female animals, remnants of a herd held on a private estate before the premises became federal property. The herd at Land Between The Lakes National Recreation Area in Kentucky/Tennessee originated in 1918 and currently numbers ≈150 animals (USDA 2008). We know of no *B. tibialis* collection records from any of the fallow deer populations in eastern North America.

In addition to the aforementioned free-ranging western North American populations in British Columbia and Point Reyes, California, smaller feral populations may occur in four or more other California counties, that is, Mendocino, San Luis Obispo, San Mateo, and Trinity (Connolly 1981, Long 2003, California Department of Fish and Game 2005); in Oklahoma (Whitaker 1996); and >10,000 fallow deer occur in Texas, as both fenced, captive animals and free-ranging herds (Mungall and Sheffield 1994, Borromeo 2002, Schmidly 2004). The earliest Texas introductions were in the 1930s, and by 1994, >20,000 *D. dama* were present in at least 93 Texas counties. The Point Reyes introductions began in 1942, but the first established and free-ranging North American fallow deer were brought to James Island, BC, Canada, from Derbyshire County, United Kingdom, in ≈1908 (Bauer 1990, Shackleton 1999), or perhaps, even earlier, in 1895 (Banfield 1977). The size of the herd on James Island in 1998 was ≈1,400 animals (Fraker et al. 2002). Sporadic historical dispersal from James Island has resulted in permanent populations today on three additional small islands also in the Juan de Fuca Strait off southern Vancouver Island, and small numbers of *D. dama* persist from an independent introduction in the 1970s on the nearby private Speiden Island (San Juan County, WA) for hunting purposes (Northwest Backroads 2005).

In addition to the several enumerated populations of feral animals across North America, fallow deer also are commonly held as captive stock in uncounted enclosures, such as deer farms, zoos, animal parks, and hunting preserves. Explosive growth of deer farming in the United States during the 1990s resulted in the redistribution of fallow deer – among several other species – to enclosure sites in nearly every state where legally permitted (Kopral and Marshall 2001). Coon et al. (2000) documented 30,000 fallow deer in enclosures belonging to members of the North American Deer Farmers Association in 1997. We have not attempted to assess the extent of *B. tibialis* presence on animals at most of these sites and premises, but based upon our findings at three Oregon deer farms and at the Hillcrest Park Zoo, we strongly suspect that such lice may be widely present wherever fallow deer occur in North America. Whitaker and Hamilton (1998) state, without specific documentation, that *B. tibialis* is among the parasites reported from resident North

American fallow deer. (All of the other parasites these authors list are native parasites of endemic American deer, however, so this statement may be based upon questionable information.)

We do have some evidence that *B. tibialis* is not always present, at least at detectable levels, on introduced fallow deer. Several book-length publications on farming fallow deer (Deegan 1991, Asher and Langridge 1992, Asher 1993) either do not mention chewing lice or dismiss them as an insignificant problem. Large numbers of introduced *D. dama* are present in New Zealand, but *B. tibialis* has never been found on them (Andrews 1973, Mason 1994, Tenquist and Charleston 2001). This absence may be the result of parasite removal during a very thorough and effective veterinary quarantine process when the founding deer were admitted to the country. Although fallow deer were the evident source of lice on BTD in the studies of Westrom et al. (1976), no lice were found on the two *D. dama* examined at the time. Promised subsequent searches for lice on additional fallow deer at the same site remain undocumented (Connolly 1981). Richardson and Demarais (1992) studied the parasites of coexisting, free-ranging white-tailed deer, fallow deer, sika deer, and chital on the YO Ranch, Kerr County, Texas, during December 1982 to January 1984. All of the parasites found were typical of those associated with white-tailed deer, and only the white-tailed deer were infested with lice. The 19 sampled fallow deer were louse free. Davidson et al. (1985) studied the parasites of free-ranging deer (sympatric *D. dama* and *O. virginianus*) in Lyon and Trigg Counties, Kentucky; they found typical endemic chewing lice on the white-tailed deer, but they did not report any lice on the fallow deer. In our own recent studies in Oregon, the digested hides of two escaped captive fallow deer, shot in 2007 outside their enclosure in Clackamas County, had no chewing lice; only three of eight individually digested hides examined from captive fallow deer in Lincoln County bore *B. tibialis;* the one sampled animal from Deschutes County was infested; and five of seven sampled deer from Linn County yielded *B. tibialis* upon individual digestion of their hides. Even in the United Kingdom, where fallow deer have lived for centuries, not all are infested. Chapman and Chapman (1975) state that the lice are present on deer in Epping Forest (Essex County), Greenwich Park (Middlesex County), and Richmond Park (Surrey County), but undocumented elsewhere. (Coincidentally, one of the slides we borrowed and studied from the British Museum of Natural History bore two female *B. tibialis* lice from Richmond Park fallow deer.) Thompson (1936) looked at "numerous skins of recently killed Fallow Deer" from Windsor Forest (Berkshire County) without finding any lice.

B. tibialis seemed never to be very numerous on their typical hosts when we digested the hides and examined the residues (Table 1), even during the cooler months of the year, when louse populations usually peak. The digestive alkali treatment of hides and hair or feathers from dead mammals or birds is a standard and convenient method for making a total parasite count on individual hosts (Hopkins 1949). As an alternative to the impractical prospect of tediously plucking each hair or feather one at a time from the entire host skin and removing any lice attached to it for a total count, digestion is the equivalent of burning down a haystack to discover its hidden needles (Clayton and Drown 2001). We found very few immature lice, possibly because they are less likely to survive the digestion process in a readily detectable state, so our counts are probably lower than true total parasite counts. But based primarily on the surviving adult lice, the highest number of *B. tibialis* found on an individual fallow deer hide was 38 females, and the range for the other hides tested individually was 0–19 lice per host. Nineteen individually digested hides yielded no lice at all. The louse numbers found in digestions of 29 hides processed in groups of three to nine hides each easily fell within that same range, when assessed on a mean lice per hide basis.

Although the previously cited study of Richardson and Demarais (1992) found no lice on Texas fallow deer, Corn et al. (1990) studied diseases of exotic ruminants, including the same four deer species, on the Edwards Plateau in Texas between November 1987 and August 1989, and they found such lice in their limited collections of parasites. Based upon identifications made at the NVSL, these authors reported that all of the ectoparasites encountered were native species usually associated with white-tailed deer, including chewing lice, *Damalinia* (*Tricholipeurus*) *parallela* (Osborn), found on all four deer species. In more informed hindsight, we question these results. Most of the louse samples upon which the identifications were based have been discarded, except for three collections from sika deer (NVSL accession 89-24247, 89-24251, 89-24252) and one from white-tailed deer (NVSL accession 90-5467). We have re-examined these specimens. The latter lice are indeed *D. parallela,* but the sika deer lice were misidentified and are actually *D.* (*Cervicola*) sp., typical Asian parasites of sika deer (sensu lato). (Note: a pair of sucking lice [Phthiraptera: Anoplura: Linognathidae], also present in one of the sika deer samples, also was misidentified at NVSL and in Corn et al. [1990] as an endemic American parasite of deer, *Solenopotes ferrisi* [Fahrenholz]; upon reassessment of the still extant lice, they are, in fact, *Solenopotes* sp. near *burmeisteri* [Fahrenholz], an exotic Old World parasite known previously from sika deer [Hopkins 1949].) According to Corn et al. (1990), 25 of 41 chital and 10 of 41 fallow deer examined in 1988 and 1989 from Kerr County also were infested with chewing lice. Although these lice are no longer available for restudy, circumstantially, we strongly suspect that they, too, were misidentified as *D. parallela.* More probably, they were really the typical louse parasites of the respective host deer, *D.* (*Cervicola*) *forficula* on the chital, and *B. tibialis* on the fallow deer. We note also that the *B. tibialis* specimens collected in the Clovis, New Mexico, zoo (Table 1) probably originated from imported Texas fallow deer. And the initial breeding stock of fallow deer at the Throop farm in Oregon, where we found *B. tibialis* present (Table 1), reportedly came from the King Ranch in Texas in 1988, although a few animals from other sources since have been added periodically. All this circumstantial evidence suggests that *B. tibialis* was present – at least in the 1980s – on deer in Texas, including at least fallow deer in Kerr County.

We have repeatedly shown throughout this discussion that the history of *B. tibialis* in North America is punctuated by a variety of misidentifications. In a number of cases, actual *B. tibialis* lice were designated as another exotic louse or as any of several endemic louse parasites of native deer. Conversely, in other instances, native cervid-chewing lice were mistakenly called *B. tibialis.* These identity problems are verifiably present in publications spanning a period of more than a century (i.e., 1896–1999). And such problems are not restricted to North America. Even European authors (e.g., Kéler 1941, Séguy 1944), in the ancestral home of this louse, for many years were prone to confuse it with another, largely sympatric species, *Damalinia* (*Cervicola*) *meyeri* (Taschenberg), from the European roe deer, *Capreolus caprelous* (L.). The latter louse species was described in 1882 (i.e., 2 yr after Piaget described *B. tibialis*). Werneck (1947) finally recognized the difficulty, unraveled the nomenclatural confusion, and attempted to set the record straight. However, one still can find instances of evident misidentification or misapplication of the *B. tibialis* name subsequent to Werneck's efforts, even in recent times (Yoshizawa and Johnson 2003, Szczurek and Kadulski 2004). And the most recent monograph on the chewing lice of the world (Price et al. 2003) only complicates the problem of correct identification because its generic key for determination of lice on Artiodactyla will place *B. tibialis* in the wrong genus (i.e., *Damalinia*), because of the anomalous anterior conformation of the head in this louse.

These unfortunate nomenclatural oversights have delayed timely recognition of the widespread presence of this exotic louse parasite in North America and retarded appreciation and serious consideration of its potential to cause problems for native deer. We see several evident and potential parallels between the North American occurrences of *B. tibialis* and *D.* (*Cervicola*) sp., the louse associated with HLS in BTD. For example, both species are exotic Old World ectoparasites unknowingly introduced to North America, probably on several occasions, along with their imported exotic deer hosts. Both species demonstrably existed here for many years and became widely distributed (note: we have many unpublished distribution records for *D.* [*Cervicola*] sp. in both western and eastern North America; see also Wilson and Durden [2003] and Nettles et al. [2002]), at least in part by human movement of infested hosts, before they were detected and correctly identified. Both have a long history of early-collected specimens that were misidentified. Both species seem to be unusual among trichodectid lice in their ability to colonize and successfully infest numerous host species (note: we also have several unpublished new host records for *D.* [*Cervicola*] sp.). This ability may be strongly tied to another highly unusual biological characteristic for phthirapterans (Marshall 1981) that is shared by these two lice, that is, both of them reproduce parthenogenetically (Westrom et al. 1976, Bildfell et al. 2004, Szczurek and Kadulski 2004). Thus, transfer of even a single individual louse in any life stage from an infested host to a new animal is hypothetically capable of establishing a viable new population. Finally, nearly all our studied collections of both species seem to present the facies of a monoculture, that is, submitted samples of these lice from infested hosts rarely contain specimens of any of the endemic lice typically occurring on native deer. This phenomenon may be evidence of competitive displacement of the endemic lice (Bildfell et al. 2004); or it may simply be sampling bias reflecting different, but unrecognized, respective anatomical or temporal infestations by the lice (Samuel et al. 1980); or it may truly reflect an immense disparity in the respective intensities of either exotic species versus any of the endemic species.

Whether this cascade of similarities leads to an association of *B. tibialis* with pathology in native cervids that parallels the HLS associated with *D.* (*Cervicola*) sp. on BTD is a continuing question. In general, the successful transfer of mammal lice from their typical host to an atypical host is a rare occurrence (Hopkins 1949, Durden 2001), but when it happens, the health consequences can be serious for the new host (Brunetti and Cribbs 1971, Foreyt et al. 1986, Bildfell et al. 2004). Among the many barriers preventing lice from heterospecific host infestations, two notable ones are at the forefront, as follows: opportunity and critical numbers. Under natural conditions, except during host-prey interactions, individuals of different mammal species usually do not associate with each other closely enough to afford their lice an opportunity to move from one species to the other. Straggler specimens of the lice of prey animals frequently are found on typical predators of those animals, but because of other secondary barriers to establishment, such occurrences are almost always ephemeral. (One exception [Clay 1976] is the case of an Australian wallaby louse, *Heterodoxus spiniger* [Enderlein], that has come to commonly infest canids and other carnivores, especially domestic dogs, *Canis lupus familiaris* L., pantropically.) The host specificity of mammal lice is promoted and maintained largely because of the ample and mostly exclusive opportunities for interhost movement afforded to them by frequent and intimate conspecific host interactions, for example, courtship, mating, birth, nursing, fighting, etc. Such frequent opportunities for movement between like hosts overcome the other initial primary barrier (i.e., critical numbers) to successful establishment of a louse infestation on a new host animal. In most cases, some minimal number (>1) of transferred individuals is necessary to found a viable population of lice on a new host animal. Hypothetically, a single mated female could serve the purpose, but practically speaking, the necessary number must surely be higher in most situations because of the low proportion of such females in a typical population and numerous other natural barriers and defenses (e.g., physical, chemical, physiological, behavioral, etc.) evolved by animals to resist parasitism. In general, only frequent conspecific host interactions allow for relatively easy and consistent transfer of lice from infested animals in sufficient numbers to establish new infestations on naive host individuals.

Evidently, both *D.* (*Cervicola*) sp. and *B. tibialis* have been able to breach the initial barriers to successful establishment on atypical hosts with some success in North America. We do not know the circumstances under which these louse movements from their exotic deer hosts to native deer occurred, but we suspect that in most cases the transfers took place under unnatural conditions that either allowed or forced the participant host animals to interact more intimately than they otherwise would have chosen; for example, captive exotic and endemic deer held together on deer farms, in zoo enclosures, or in experimental pens (Westrom et al. 1976, Robison 2007); fraternization of free-ranging endemic deer with exotic captives through enclosure fencing (VerCauteren et al. 2007); feral animals sharing ranges on wildlife preserves or small islands (Cowan 1946, Hopkins 1960); or possibly wild/feral animals drawn to and concentrated at human-provided feeding sites. One other possible means of transfer from an infested host to a naive host is phoresy via one of the two species of deer keds (*Lipoptena depressa* [Say] and *Neolipoptena ferrisi* [Bequaert] [Diptera: Hippoboscidae]) that commonly move among all cervids in the western states (Bequaert 1957). Phoresy on louse flies is known for many bird lice (Keirans 1975a), but the only reported deer louse phoront is *D.* (*Cervicola*) *meyeri* on mosquitoes and a muscid fly in Europe (Keirans 1975b, Nielsen 1990). The role of louse phoresy in the present situation is unexplored.

In any case, the parthenogenetic nature of these two louse species facilitates success of the initial jump to a new host species because the critical number for them to establish and reproduce is always only one individual louse (or very few), without regard to sex, age, mating status, or life stage. Even so, the initial successful jump from one host species to another probably does not occur very frequently, given the generally low intensities of lice on their typical hosts. With respect to *B. tibialis* and *D.* (*Cervicola*) sp., all of the observed atypical hosts have been cervids, and evidently the habits and biological and nutritional requirements of both lice are sufficiently unspecialized to allow them to survive the secondary defenses of and thrive on animals only as taxonomically removed from their normal hosts as are other kinds of deer. Thus, once the initial colonization has succeeded, these lice seem to be preadapted to their adopted new hosts and circulate there like the normal, endemic louse parasites of those hosts, in that they are easily transferred from one individual to another during ordinary conspecific host interactions, and they can spread freely through a local host population.

We do not know why, but among exposed cervids, *O. hemionus* seems to be particularly vulnerable to colonization by both species of exotic lice, that is, *B. tibialis* and *D.* (*Cervicola*) sp. Nevertheless, cross-contamination from the typical hosts of these lice is not always assured. If it were, pathologically significant pediculosis – or at least exotic louse collections – in *Odocoileus* deer might have been more prominent and common over the last hundred years of exposure. In their study of free-ranging and captive BTD pastured with fallow deer, Westrom et al. (1976) found that only three of the 71 examined BTD were infested with *B. tibialis.* The infested deer were among 19 examined captives that directly or indirectly shared enclosures with fallow deer. Ten fallow deer were present on the premises, only two of which were examined for parasites; both were louse free. Our own observations from Point Reyes, California, may prove instructive in this regard, as well. Four species of cervids currently share the range at Point Reyes, as follows: adventive chital and fallow deer, and native BTD and tule elk, *Cervus canadensis nannodes* Merriam. Until recent active population reductions of the exotic species, they possibly outnumbered the endemic species. To date, we have examined multiple samples of ectoparasites from only the exotic deer, and both species are infested at low levels with their typical exotic chewing lice (i.e., *D. forficula* on chital and *B. tibialis* on fallow deer). One observation to date leads us to believe that at least BTD and fallow deer on this range do associate with each other to some degree. In an ectoparasite sample from one fallow deer, we found and identified one male *Damalinia* (*Tricholipeurus*) *odocoilei* (McGregor), a typical and common chewing louse on *Odocoileus* deer in western North America (Werneck 1950). The presence of an endemic louse on an exotic host suggests that interspecific host contacts probably are sufficient enough to allow converse movement of exotic lice to native hosts, as well.

For many years, populations of both BTD and tule elk at Point Reyes were possibly smaller than those of the exotic deer species, giving the native species ample exposure to parasites from the exotics. Until recently, neither we nor park personnel had noted any unusual or serious signs of pediculosis on local native cervids. However, during the winter of 2008–2009, a notable number of elk showed signs of extensive hair loss (N. B. Gates, personal communication). The cause of this widespread condition has yet to be determined, but earlier, in March 2008, a single Point Reyes tule elk found dead of natural causes was necropsied, and a sample of 42 lice was collected from it. At NVSL (accession 545539), J.W.M. identified these lice as *Damalinia* (*Cervicola*) sp., the same louse associated with HLS in BTD in the Pacific Northwest. How this third species of exotic cervid-chewing louse came to be as far south as Point Reyes is unknown, and whether it or one of the other two introduced lice on site is responsible for tule elk alopecia is still a collateral open question, as well. Hair loss has not been observed in BTD at Point Reyes, but perhaps this is due more to the local scarcity of these deer than to absence of lice on them (N. B. Gates, personal communication).

Even though we know that *B. tibialis* has been present on native deer in western North America since at least 1941 (Table 1), and possibly since early fallow deer introductions in 1895 or 1908, we could not unequivocally show that these lice had caused health problems for the deer until 2005. As shown by Bildfell et al. (2004), the studies of Cowan (1946) purported to deal with endemic chewing lice on BTD in British Columbia, but the observations may have been compromised to some degree by the unrecognized presence of exotic *B. tibialis* in the studied populations of deer. Cowan reported that many of his subject animals had intense louse infestations and showed clinical signs similar to those seen today in deer with HLS, but we cannot determine at this late date whether those afflicted animals were infested with endemic lice, as alleged, or with misidentified *B. tibialis.* Endemic lice on their typical, healthy wild animal hosts usually occur at low intensities and without noticeable health consequences (Durden 2001). In fact, studies of endemic *Damalinia* (*Tricholipeurus*) spp. lice on their typical host white-tailed deer have concluded that intensities as high as 70,550 lice per animal are not necessarily inimical to the hosts (Samuel and Trainer 1971, Watson and Anderson 1975, Samuel et al. 1980). Westrom et al. (1976) counted a maximum of 8,200 *B. tibialis* on one of their infested BTD, but these authors did not comment on any health consequences. Those numbers far exceed anything we found for *B. tibialis* on any of the fallow deer we examined (Table 1).

Our 2005 observations in Washington (Table 1) of hybrid BTD × MD infested with *B. tibialis* suggest that hair coat condition was only slightly affected on individual hosts infested with no more than 100–200 lice each, but it varied inversely with louse intensity. The 2006 samples were from a road-killed animal, a deer found dead of unknown causes, and two animals selected for lethal removal and examination because of noticeably severe hair loss. We did not actually count lice on these deer, but we estimate that each sustained thousands of insects. The lice on the recently dead deer had clustered together in little mounds on the host's shoulder.

In the wake of the sweeping tide of HLS associated with exotic *Damalinia* (*Cervicola*) sp. lice on BTD in the Pacific Northwest, we think it is prudent to take note of the presence of *B. tibialis,* another similar exotic deer louse, in the same region and probably elsewhere in North America, in case it should engender similar problems for native deer. The fact that *B. tibialis* probably has been unobtrusively present in North America for a much longer time than the *Cervicola* lice might suggest that its potential to cause such problems may not be as great. However, one observation of farmed fallow deer in Denmark (Jorgensen and Vigh-Larsen 1988) shows that, even on its typical host, this louse occasionally might be involved in yearling mortality with clinical signs that are uncomfortably similar to those in HLS of American BTD. And, in fact, the latest observations we have in south-central Washington strongly indicate that *B. tibialis* infestations on BTD × MD hybrid hosts may lead to significant hair loss, fawn mortality, and host population reduction.

Recent Developments. During the time between the end of our formal survey activities for chewing lice on western state cervids and the completion of the manuscript for this study, we accumulated some additional information on *B. tibialis* that tends to support some of the conclusions and projections arising from our original work.

One of us (J.A.B.) continued observation and assessment of local hybrid deer populations in south-central Washington, collecting more lice that we identified as *B. tibialis* from additional counties, that is, Benton County (NVSL accession 555728) and Klickitat County (accession 09-4457). Unpublished data of wild deer herds in the local wildlife management area where lice were initially encountered suggest the health problems we feared are coming to pass. Since the discovery of *B. tibialis* there in 2005, district-wide deer populations have declined in Yakima and Kittitas Counties by an estimated 40–50%, and deer with hair loss have been found in all corners of the district (Washington Department of Fish and Wildlife 2009). The decline is quick, but patchy; one area may lose 70% of its deer, but an adjacent area may be virtually untouched. Areas not affected previously now show high incidences of deer with signs of hair loss. Areas with previous population declines have not recovered. Animals that seem phenotypically 100% mule deer are notably as vulnerable as the evident hybrids. In many ways, HLS in this population of hybrid deer is following the pattern observed with *D.* (*Cervicola*) sp. lice on BTD, including the fact that fawns are the most likely to suffer from it. The most recent *B. tibialis* sample (accession 09-7252) from Washington came in April 2009 on a pure-bred Rocky Mountain mule deer with extensive alopecia; it was road killed near Wenatchee, in Chelan County, another new distribution record for *B. tibialis.*

In April 2008, one of us (J.W.M.) received and identified samples of *B. tibialis* lice collected from two pure-bred Rocky Mountain mule deer found dead in Badlands National Park, Jackson County, South Dakota (accession 551020 and 555719). The host animals were heavily infested with lice, emaciated, and showed a high degree of hair loss. These collections established new state and county distribution records, a new host record, and further evidence that *B. tibialis* may be associated with mortality of endemic American deer.

Such evidence grew even stronger in the spring of 2009, when J.W.M. received and identified numerous additional *B. tibialis* samples from MD in the same area of South Dakota (Jackson and nearby Custer Counties) and from four new western localities, three of them in new states. All collections were associated with severe alopecia, morbidity, and mortality in the MD hosts. New distribution records are as follows: Tuolumne County, California (accession 09-4135); Idaho County, Idaho (accession 09-3721); Box Butte

County, Nebraska (accession 09-4213); and Carbon County, Wyoming (accession 09-4212). The California collections were from a new host subspecies, California mule deer (*O. hemionus californicus* [Caton]), and were associated with a widespread die-off of deer with severe alopecia. All other new records were from Rocky Mountain mule deer hosts.

Finally, we recently obtained evidence that *B. tibialis* still persists on Vancouver Island, BC, Canada, 60 yr since the last known collection there. A routine sample of lice (accession 09-16429) submitted to NVSL for identification and collected in December 2008 from a BTD in the Nanaimo area contained 30 female *B. tibialis.* The last and only previous record we know of from Vancouver Island dates to 1948 at Campbell River, 120 km to the north (Table 1).

Accumulating evidence suggests that *B. tibialis* may be following the pattern established by *Cervicola* sp. (Foreyt et al. 2004, Bildfell et al. 2004) in causing widespread alopecia and inimical consequences for the health of endemic American deer herds in the western United States. Why this is occurring now, after at least 65 – or perhaps >100 – years of low-profile *B. tibialis* presence in the region, is an open question. We note that MD subspecies and hybrids are the most recently infested taxa, and they seem to be hardest hit, suggesting that they are more vulnerable than are BTD subspecies exposed in earlier times. To date, white-tailed deer in the West seem uninfested and unaffected. We also note that, unlike previous collection records from native deer, to date, none of the most recent infestations on MD has been positively associated with nearby fallow deer as sources for *B. tibialis.*

Although the pathological consequences associated with the exotic sucking louse, *Linognathus africanus* Kellogg and Paine (Phthiraptera: Anoplura: Linognathidae), for western deer never became as widespread as those seen with the two exotic chewing lice, they were qualitatively similar on individual affected hosts (Brunetti and Cribbs 1971). Because of the evident similarities in the diseases associated with presence of *L. africanus, B. tibialis,* or *D.* (*Cervicola*) sp. on multiple endemic cervid hosts, we propose a new, general name and acronym to cover the condition, without regard to louse or host species involved, that is, exotic pediculosis of deer (EPOD). The future health of western American deer herds seems to be increasingly tied to the prevalence of EPOD, although we are aware that the near simultaneous rise and spread of adenovirus hemorrhagic disease of deer in the same region (Woods et al. 2008) may complicate analysis of this situation.

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