School of Graduate Studies
Bemidji State University
1500 Birchmont Dr NE, #48
Bemidji, MN 56601-2699
(218)-755-2027

MOVEMENT ACTIVITY OF BURBOT, (*MIZAY; LOTA LOTA*) IN A SPRING-FED MINNESOTA LAKE

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Abigail M. Fountain

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APPROVAL BY THESIS ADVISOR

THIS THESIS HAS BEEN APPROVED ON THE DATE SHOWN BELOW:

13 Jan 2025

Andrew W. Hafs, Ph.D.
Committee Chair
Professor of Biology

Date

Feb 10, 2025

Dean, College of Business, Mathematics & Sciences

Date

MOVEMENT ACTIVITY OF BURBOT, (*MIZAY; LOTA LOTA*) IN A SPRING-FED MINNESOTA LAKE

Abigail M. Fountain

Burbot (*Mizay; Lota lota*) are a relatively unmanaged freshwater fish, important in many local Indigenous cultures, but often overlooked or maltreated in research, conservation, and fishing practices. As such, relatively little research has been conducted on Burbot, despite ecological significance as an indicator species. A recent resurgence in popularity as a target species, however, has prompted new research to inform management policies. The objectives of this study were to summarize Burbot movement by identifying patterns in swimming activity and identify possible predictors of the movement observed. This study investigated the movements of 39 individuals implanted with acoustic transmitters in Bad Medicine Lake, Minnesota, over a period of 18 months. Movement rate and turning angle were calculated for each transmission interval and analyzed using mixed-effects modeling. Seasonally, changes in movement patterns occur around ice-on, ice-off, and spawning events, varying in magnitude across sex and diel period. Nightly increases in movement persist regardless of season. Overall, movement activity was best predicted by the interaction between sex, diel period, and season. However, it is likely that movement patterns observed are influenced by the interaction of additional biological, behavioral, and environmental factors.

Approved by:

13 Jan 2025

Committee Chair

Date

Shannon Fisher Digitally signed by Shannon Fisher
Date: 2025.01.14 08:49:12 -06'00'

Committee Member

Jon E Anderson 14 Jan 2025

Committee Member

Carl Isaacson 1/15/2025

Graduate Faculty Representative

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* * *

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MOVEMENT ACTIVITY OF BURBOT, (*MIZAY; LOTA LOTA*) IN A SPRING-FED MINNESOTA LAKE

Introduction

Movement activity within aquatic systems is difficult to observe and quantify [1, 2]. The behavior that influences this movement, especially how it relates to environmental changes, is even more difficult to observe and quantify, especially through direct observation [3, 4]. However, advances in research methods and technology have allowed for a new understanding of these behaviors. In particular, the development and implementation of new tracking and analysis techniques enables a more complete and in-depth analysis of fish movement behavior within aquatic systems. Understanding fish movement is crucial to understanding fundamental population dynamics, including population genetics, structure, and distribution [5]. Previously, movement was tracked exclusively through mark-recapture, but new techniques increasing in popularity include passive integrated transponder (PIT) tags, hydroacoustics and sonar, otolith microchemistry and isotope analysis, and radio or acoustic telemetry [6]. Telemetry in particular has a wide scope of applications including reproductive biology, environmental interactions, habitat use, invasive species, diet and trophic niches, and fish passage. Telemetry technology allows for indirect observation of individuals across large habitats and long study periods. Applying these techniques to Burbot (*Mizay; Lota lota*) specifically, a poorly understood species and indicator of ecosystem health, allows for a better understanding of aquatic ecosystems.

Movement can be quantified in a variety of ways. Swim velocity, which is a measure physical capability, is categorized as (1) maximum velocity, the highest possible velocity in a short burst, or (2) critical velocity, the highest velocity that can be maintained for a prolonged period. Critical velocity, often expressed in terms of body lengths, varies by species. An experiment conducted by Jones, Kiceniuk, and Bamford [7] used a 10 min swim test to quantify critical swim velocities through length-velocity regressions [7]. The fitted curves suggests White Suckers (*Catostomus commersonii*), a native benthic species like Burbot, can sustain a swimming velocity up to 3,200 m/h, whereas neither Burbot nor Northern Pike (*Esox* *lucius*) can sustain velocities greater than approximately 1,600 m/h for 10 min. In addition, unlike the majority of fish species, length had no relationship with critical swim velocity in Burbot [7]. In addition to measuring swim velocities, movement activity can be quantified using movement rates. Rather than physical ability, movement rates describe the amount of movement exhibited *in situ* within a given time period, and they have been documented extensively for many common game species. Walleye (*Sander vitreus*) have been known to move, on average, between 200 and 450 m/h, with a significant increase in movement at dusk and night [8, 9]. Northern Pike also display these patterns of crepuscular activity [10, 11]. Moving less than 50% of a 24 hour period, with a significant decrease of activity in winter, Northern Pike move, on average, 1 to 2.5 km per day, or approximately 40-105 m/h [12]. In comparison, Burbot movement averages 0.85 km per day, or 35 m/h, also with significant increases in activity at night [13]. Despite their nightly activity, Burbot have quite low swimming endurance [14]. Movement rates, when combined with spatial use, habitat, and bioenergetic analyses, can further provide insights into resource requirements, energy expenditures, and the broader ecological role of the specific species.

Native to Minnesota, Burbot are easily recognizable with olive-brown to black coloring, an eel-like laterally compressed body, and flattened head [14]. The only member of order Gadiformes to be found in freshwater, they have the largest range of any freshwater fish with circumpolar distribution across the Northern Hemisphere [13, 14, 15]. In these systems, Burbot are benthic-dwelling predators with a diet composed primarily of fish and, to a lesser extent, aquatic invertebrates [14, 13]. They inhabit cool rivers and deep lakes where they often remain below the thermocline. In late fall, as water cools, Burbot in lentic systems migrate extensively from the benthic regions of the hypolimnion to shallower waters [14]. This migration, called diel bank migration, is a form of diel activity where Burbot remain close to the bottom but transition from deeper water during the daytime to shallower water at night, where they feed or spawn [13]. During spawning in late winter or early spring, Burbot are known to have increased home-range sizes indicating regular movement on a greater scale, likely a reflection of increased diel migration [14, 16].

Burbot were and continue to be desired by many Indigenous Peoples. Traditional food, defined as food that is culturally accepted and available from local natural resources, and the activities associated with harvesting these foods are an integral part of local indigenous culture [17]. Value in traditional diets, proliferated by community elders, is rooted in nutritional and health benefits. As a staple in Ojibwe diets, Burbot were traditionally harvested using a variety of methods, including weirs, traps, nets. Burbot liver, considered a delicacy in some indigenous cultures, is specifically known to have health benefits. The liver must be eaten in addition to muscle to obtain necessary fatty acids, due to the low level of fat in muscle tissue of Burbot [18]. Traditionally almost all parts of an animal were consumed, making these essential nutrients available to consumers [18]. In addition to improved health, nutrients in traditional food are crucial for preserving cultural identity and promoting a sense of self-worth, as food is seen as a gift from the Creator [18, 17].

After the invasion of North America by Europeans and the later development of organized conservation efforts, Burbot were commonly excluded from research and management practices due to a decrease in popularity as a sport and commercial fish [14, 15, 19]. Despite declining and endangered population numbers worldwide, little is known about Burbot behavior. Recent research suggests sex, diel periods, season, and individual difference influence movement behavior. Previous studies have investigated Burbot activity level and home range, but few have quantified how fast, how often, or in what manner these fish are moving, especially in closed or lentic systems. An affinity for cold water, combined with their benthic nature, make these patterns unique and particularly interesting to study [13]. Burbot are ideal organisms for aquatic ecology research because their sensitivity to environmental change and high trophic level make the species great indicators for environmental stress and overall ecosystem health [19]. The development and implementation of new tracking and analysis techniques in movement ecology enables in-depth study of difficult to observe phenomena in Burbot. As indicators of ecosystem health, a better understanding of Burbot allows for a better understanding of aquatic ecosystems as a whole. The main objectives for this study were to describe daily and seasonal patterns of movement activity, and to quantify the relationship between movement activity and sex, season, diel period.

Methods

Study Design

Data were obtained according to the methods outlined by Robinson et al. [16]. Burbot were caught and surgically implanted with V9TP-2L transmitters (Innovasea, Vemco Ltd, Halifax, Canada) between March 28 and May 2, 2019. A corresponding array of 38 VEMCO receivers was deployed in Bad Medicine Lake on April 6, 2019. Data were recorded until the removal of receivers on September 28, 2020. Of the 66 individuals tagged, a majority of transmitters (n = 60, 90%) had a delay of 880-1,080 s, with an additional six (10%) having a 300-420 s delay. Following the conclusion of the study, data downloaded from receivers were sent to VEMCO for geographic coordinate estimation with the Vemco Positioning System (VPS) analysis protocol [20, 21].

Data Processing

Prior to analysis, data were filtered for accuracy based on predetermined constraints for date, abnormal activity, and positioning error. First, all transmissions before May 15, 2019, were excluded from analysis to eliminate any influence the surgical procedure may have had on behavior. Extended periods of abnormal activity, identified through a combination of path animations and depth plots, were used to assign fate and determine tag rejection for each individual [5, 13]. Tags that remained in the system with normal activity were defined as "alive", whereas tags that had depth readings that remained constant for an extended period (over 24 hours) with very little lateral movement were defined as "presumed dead". Lastly, tags that disappeared from the system before the end of the study, or those with inaccurate reading (ie. depth of -1 m for over 24 hours) despite normal patterns in lateral movement, were defined as "unknown". For individuals that remained in the system but were presumed dead or fate unknown, transmissions up to the start of abnormal activity were included in analysis. Therefore, as the study length progressed, the number of detected individuals decreased.

Each transmission included a unitless measure of hyperbolic positioning error (HPE). Methods developed by Smith [22] as cited by Meckley et al. [23] were used to evaluate positioning error by calculating the twice distance root mean square error (2DRMS) using a reference transmitter placed within the system. A linear regression relating HPE in 1-unit bins to the 2DRMS error quantified the relationship between HPE and positioning error in meters for three seasons: open water of 2019, the period of ice-on between 2019 and 2020, and open water of 2020. Across all three seasons, positioning error was less than 11m with 75% of data being retained. All calculations and analyses were conducted in R (version 4.2.2) with RStudio (version 2023.09.1.494) [24, 25]).

Calculations

Interval distance and turning angle were calculated using the moveHMM package (version 1.8) for R [26]. Total distance travelled between 2 transmissions was calculated using equation 1.

$$\overline{T_i T}_{i+1} = \sqrt{(x_{i+1} - x_i)^2 + (y_{i+1} - y_i)^2} \tag{1}$$

Where (x_i, y_i) is the position at transmission i, T_i, and (x_{i+1}, y_{i+1}) is position at transmission $i+1$, T_{i+1}. A movement rate R_k for interval k, was then calculated by dividing total distance, $\overline{T_i T}_{i+1}$, by the time elapsed between T_i and $T_i + 1$, I_k (hereafter "transmission interval"; equation 2).

$$R_k = \frac{\sqrt{(x_{i+1} - x_i)^2 + (y_{i+1} - y_i)^2}}{I_k} \tag{2}$$

This rate assumes straight-line movement between transmissions, and therefore the accuracy relies, in part, on the length of time interval. Preliminary investigation showed evidence of non-consecutive pings, typical of fine-scale acoustic telemetry data, causing longer time intervals between detections. As a result, distance traveled and movement rate should be interpreted as minimum estimates. Movement rates exceeding the maximum swimming velocity of Burbot, determined by Jones, Kiceniuk, and Bamford [7], were removed from analysis. Subsequently, turning angle was calculated by taking the absolute value of the angle between the direction traveled in interval a and the direction traveled in interval $a+1$. Thus, a fish moving in the same direction for two consecutive intervals would have a turning angle of 0°, and a fish moving in opposite directions in consecutive intervals would have a turning angle of 180°.

Diel period was assigned (day or night) using the initial detection time of an interval. Sunrise and sunset times were retrieved from the sunCalc package (version 0.5.1) for R [27].

Movement activity (movement rate and turning angle) for which the transmission intervals exceeded 485 min were removed to avoid one interval spanning several diel periods, as 485 min is the shortest day/night period within the study. Seasons were assigned (open or ice) based on the ice-in on December 2, 2019 and ice-out on April 29, 2020 from the Minnesota Department of Natural Resources (MN DNR) Lake Ice Out/In Report [28]. Dates were collected by the Minnesota Pollution Control Agency and MN DNR Lake Level Monitoring Program, respectively.

Data Analysis

Summary statistics for movement rate were calculated by finding the daily median movement rate for each individual, then taking the median of daily movement rates for all individuals within a week. Interquartile range (IQR) was calculated by finding the difference between the 75th and 25th percentiles of daily movement rates. Due to the bimodal distribution, summary statistics for turning angle were calculated by binning turning angle in 10 ° intervals and taking the daily binned mode for each individual. Then, the median and mode was calculated for daily modes of all individuals within a week. IQR was calculated by finding the difference between the 75th and 25th percentiles of daily binned modes.

Additive and interactive linear mixed-effects models were used to test if sex (female or male), diel period, and season significantly predicted movement rate and turning angle respectively. The transmitter identification number, unique to each individual, was included as a random effect on every model. Model development was done using the lme4 package (version 1.1.32) and small sample size corrected Akaike information criterion (AICc) was used to determine the best supported model [29, 30]. In addition, the correlation between movement rate and turning angle was described using a linear model, with weekly median movement rate as a predictor for weekly median turning angle.

Results

Of the 66 tagged Burbot, 39 individuals, 18 female (382-845 mm) and 21 male (366-609 mm), were used in analysis. Of the 374,036 total transmissions between May 2019 and September 2020, 56% (n = 208,698) were females and 44% (n = 165,338) were males (Table 1). Transmissions were split equally among day (48%, n = 178,384) and night (52%, n

= 195,652). Nearly half (48%, n = 177,931) of the transmissions occurred during open water of 2019, 19% (n = 126,789) were during the ice-on, and 34% (n = 69,316) occurred in the open water season of 2020. Movement rate exceeded the maximum swim velocity for Burbot in 6,015 transmissions, which were removed prior to analysis [7].

Movement Rate

Median (IQR) movement rate of all individuals across the entire study period was 29.5 m/h (8.0–90.0), though movement rate varied between sexes, diel periods, and seasons (Table 2). Overall, female median movement rate (38 m/h, 13-78 IQR) was less than males (39 m/h, 12-81 IQR), and movement during the day (20 m/h, 7-43 IQR) was less than night (62 m/h, 31-109 IQR). Median daytime movement rate for females was relatively constant within a season, though a noticeable decrease occurred just before ice-on (Figure 1). Rates then remained constant throughout ice-on and increased just after ice-off in spring of 2020. Males had a similar pattern, but with an additional peak in daytime movement in late winter. In contrast, nighttime movement of both sexes had more weekly variation but little seasonal variation, with a notable increase in IQR of both females and males during late winter. Seasonally, median movement rate decreased from 42 m/h (18-83 IQR) during open water to 23 m/h (8-70 IQR) during ice-on. There is evidence of an interactive relationship between the effects of season and diel period on movement rate, as the greatest difference between daytime and nighttime median movement rate occured during ice-on (Figure 2). The best supported model included sex, season, diel period, and interactions between (1) sex and season, (2) sex and diel period, (3) season and diel period, and (4) sex, season, and diel period (Table 3). Predictor estimates suggest movement rate is greater for males compared to females, at night compared to daylight, and during both open water seasons than during ice.

Turning Angle

Turning angle across the entire study period was bimodally distributed, with a mode of 175° and a median of 95° (35-155 IQR). Overall, females and males had equivalent median turning angles (95°, 35-155 IQR), yet daytime median turning angle (105°, 135-165 IQR) was greater than night (85°, 25-155 IQR). Daytime median turning angle for both sexes varied most notably by season, measuring approximately 90° or less from May 2019 until ice-on, when it increased to around 150°, then remained relatively constant until it decreased around ice-off in the spring (Figure 3). At night, median turning angle for both sexes also increased slightly during ice-on going from less than 90° during open water to greater than 90° during the ice-on season. During ice-on there was much more weekly variation in median turning angle than either open water period. There is also evidence that median turning angle increases during daylight hours in ice-on season, whereas turning angle during both open-water seasons remains relatively constant across all hours of the day (Figure 4). Overall, median turning angle during open water (75°, 25–145 IQR) was less than ice-on (135°, 55–165 IQR). The best supported model included sex, season, diel period, and interactions between (1) sex and season, (2) sex and diel period, (3) season and diel period, and (4) sex, season, and diel period (Table 4). Predictor estimates suggest turning angle is greater for males compared to females, during daylight compared to night, and during ice compared to either open water season.

Relationship of Movement Rate and Turning Angle

Preliminary plotting showed seasonal changes in daytime movement rate and turning angle at approximately the same times of year, so that as movement rate decreased median turning angle increased (Figure 5). A linear regression was used to investigate this relationship, testing if movement rate significantly predicted turning angle. The fitted regression model was significant during the day for both females ($P < 0.001, R^2 = 0.71$) and for males ($P < 0.001, R^2 = 0.73$), but not significant at night for either sex ($P = 0.063, R^2 = 0.046$; $P = 0.176, R^2 = 0.025$).

Discussion

This study identified distinct patterns of Burbot movement activity influenced by both biological and environmental factors. Seasonally, changes in movement patterns occured around ice-on, ice-off, and spawning events, varying in magnitude across sex and diel period. This is consistent with documented seasonal variation in home and core range of Burbot, with individuals inhabiting significantly larger areas before and during the spawning window [16, 31]. However, nightly increases in movement persisted regardless of season, consistent with diel migration behavior previously identified in Burbot populations [13, 32]. The data also showed a decrease in daytime median turning angle as daytime median movement rate increases, indicating movement, though minimal, throughout rest periods. Several ecological and behavioral implications that can be drawn from the data presented in this study.

Consistent changes in movement activity are observed daily and seasonally, comparable to other native species. Overall, observed Burbot activity was higher at night compared to day across both sex and season. This nightly increase in median movement rate is consistent with previously documented nightly increases in vertical movement, horizontal movement, and acceleration [13]. The increase is likely a consequence of increased diel bank migration, documented extensively in Burbot populations [13, 5, 33, 32]. Seasonally, Burbot activity increases in late winter due to behavioral changes during spawning. Changes in movement behavior in and around the spawning period is not unique to Burbot, as maximizing reproductive effort elicits seasonal migratory movement in many fish species [34]. Migratory movements across a range of spatial and temporal scales have been documented in many taxa of native freshwater fish, including several key game species in Minnesota. However, the late-winter spawn of Burbot occurs drastically earlier within the calendar year than the spring or fall spawning of other popular game species. These nightly and seasonal patterns make Burbot populations uniquely vulnerable to overfishing, as most Burbot angling occurs during nightly spawning aggregations in late-winter [13, 35]. Additionally, when combined with previous spatial analysis of these data, the observed activity revealed relatively localized movement within the system. Home range analysis showed that outside of the spawning period, Burbot on Bad Medicine Lake spend, on average, 90% of time within an area of less than 1 km^2 and 50% of time within 0.25 km^2 [16]. However, median nightly movement rates up to 125 m/h indicate Burbot swam as far as 1 km in a single evening. Therefore, an increase in movement activity does not indicate high spatial usage or large migratory movements within the system, but relatively localized movement. Individuals within this system seldom underwent long distance travel, rather they exhibited repetitive movement within a specific area, which varied in size and location throughout the year. The diel bank migration behavior observed in Burbot individuals further suggests that true movement rates were greater than horizontal movement alone, as extensive vertical movement has been repeatedly documented [5, 13]. Combined with a relatively low critical velocity and endurance of the species, this behavior may explain why Burbot often inhabited areas with dramatic changes in water depth [7, 16]. Further investigation identifying and describing the hot spots where localized movement occurs will identify necessary habitat and reveal potential vulnerabilities of the species.

During the day, Burbot were often resting with bouts of limited activity, possibly in response to disruptions. This pattern is illustrated by the relationship between turning angle and movement rate, such that during daylight hours, median turning angle decreased as median movement rate increased. Though this appears contrary to the localized movement described above, it is important to note this pattern is only significant during the daytime, when the least amount of movement activity occurs. Previous studies have established daylight hours as a known period of decreased activity in Burbot, consistent with decreased median movement rates during the day when compared to night [13, 5]. Specifically, from just before ice-on to the proposed spawning window, observed weekly movement rates were low and turning angles high. This period of decreased activity is consistent with resting behavior, in which distance traveled by an individual was minimal. However, the heading of the individual changed frequently, suggesting Burbot likely remained alert throughout periods of rest and inactivity. Frequent turns with low movement rates may be interpreted as *pseudo*-vigilance behavior, whereupon individuals maintained awareness of the surrounding environment, despite decreased activity. On the other hand, from late winter until fall, daytime movement rates increased and turning angle decreased, though activity was still less than that at night. This increase in activity during resting periods may have been a response to disruptions. These disruptions, environmental or anthropogenic, are more likely to occur during the open water season and likely result in a short, straight burst to a new resting location. Notwithstanding, it should be noted that these interpretations should be made with caution. Positioning error may result in intervals with a true movement rate of 0 m/h to have small, non-zero movement rates. Thus, any distance of travel less than that of the established positioning error may have been confounded. This can be mitigated by (1) utilizing transmitters with a shorter transmission interval or (2) decreasing the acceptable positioning error. As this was an existing data, changes in acoustic telemetry methods were not considered in this study. Decreasing the acceptable margin of error was considered but deemed inappropriate for the scope of this investigation. Decreasing positioning error significantly reduced the total number of transmissions, resulting in a greater median transmission interval. Subsequently, the underestimation of movement rates due to the assumption of straight-line travel was amplified, decreasing the accuracy of the results.

Relatively minimal differences in movement activity were observed between females and males, despite the most parsimonious models for both movement rate and turning angle including sex as a predictor. There are three likely explanations for the observed pattern. First, the differences in movement activity by sex were small in magnitude, yet these small effects become important predictors of movement due to the frequency at which they occurred. The quantity of data used in this study is immense, increasing the power to detect small effects. Therefore, the impact may be statistically significant but the magnitude of the effect unimportant. Additionally, it is possible that sex improved model fit due to the importance of the interactive term. The difference in movement rate between females and males was largest in magnitude during March of 2020, the proposed spawning season for this population (Figure 1). Thus, the model with the most support included sex as a predictor of movement activity due to the significant interaction with season. Lastly, the significance of sex as a predictor of movement activity may be confounded.

Our best supported model provided evidence to suggest movement activity was best predicted by sex, diel period, season, and their interactive effects, though it is also likely the interaction of additional biological, behavioral, and environmental factors are important predictors of movement activity. Studies on another bottom-dwelling, freshwater species, the European catfish (*Silurus glanis*), and freshwater and anadramous salmonid populations, including Arctic Charr (*Salvelinus alpinus*), Brook Trout (*Salvelinus fontinalis*), and Atlantic Salmon (*Salmo salar*), have shown that movement activity increased in response to limited resource availability, oxygen deficits, and warmer water temperatures, factors which may also be particularly important for Burbot populations in closed-systems [36, 37, 38, 39, 40, 41, 42]. Movement in these species also increased with increased habitat size and an increase in length or body condition [37, 42]. Specifically, in intraspecific interactions, individuals with smaller relative size had greater movement activity than larger individuals [36]. Relative size could be an important predictor of movement of Burbot within the spawning window, as spawning aggregations result in many individuals in a central location, and thus increased occurrences of intraspecific interactions. Conversely, movement activity in the mentioned freshwater species decreased with familiarity or prior residency of an area [36, 42]. Further investigating these along with other possible unidentified factors and their relative impact on movement behavior will facilitate a better understanding of the ecological needs and potential vulnerabilities of Burbot populations. As a result, population assessments and resulting conservation actions will be more accurate and effective. Developing and implementing effective management strategies are imperative to maintaining robust Burbot fisheries amidst global population decline.

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Tables

Table 1

Female, male, and total acoustic transmission frequencies (% of 374,036 signals) from 39 Burbot in Bad Medicine Lake, Minnesota, between April 2019 and September 2020. Detection frequencies are divided into three temporal periods, including open water in 2019 (Open 2019), the ice-covered period between 2019 and 2020 (Ice On), and the open water in 2020 (Open 2020). For each cell the percentage of total detection and number of detections is reported.

	Sex		
Diel Period	**Females**	**Males**	**Total**
Open 2019			
Day	13% (47,707)	10% (37,872)	23% (85,579)
Night	14% 51,967)	11% (40,385)	25% (92,352)
Total	27% (99,674)	21% (78,257)	48% (177,931)
Ice On			
Day	9% (31,994)	8% (28,229)	16% (60,223)
Night	10% (37,066)	8% (29,500)	18% (66,566)
Total	18% (69,060)	15% (57,729)	34% (126,789)
Open 2020			
Day	5% (18,691)	4% (13,891)	9% (32,582)
Night	6% (21,273)	4% (15,461)	10% (36,582)
Total	11% (39,964)	8% (29,352)	19% (69,316)
Total			
Day	26% (98,392)	21% (79,992)	48% (178,384)
Night	29% (110,306)	23% (85,346)	52% (195,652)
Total	56% (208,698)	44% (165,338)	100% (374,036)

Table 2

Movement rate medians and interquartile ranges (IQR; m/h) and turning angle medians, IQRs, and modes (degrees) for 39 Burbot in Bad Medicine Lake, Minnesota, between May 2019 and September 2020. Movement data are reported by sex, water conditions (open water and ice-covered periods), and diel period. Turning angle modes were calculated using 10° bins.

	Movement Rate (m/h)		**Turning Angle (degrees)**		
Group	**Median**	**IQR**	**Median**	**IQR**	**Mode**
Sex					
Females	38	13-78	95	35-155	175 (13% , n = 2,180)
Males	39	12-81	95	35-155	175 (12% , n = 1,647)
Diel Period					
Day	20	7-43	105	135-165	175 (15% , n = 2,063)
Night	62	31-109	85	25-155	175 (11% , n = 1,764)
Season					
Open	42	18-83	75	25-145	175 (22% , n = 1,858)
Ice	23	8-70	135	55-165	175 (9% , n = 1,969)

Table 3

Small-sample corrected Akaike information criterion (AICc) values and difference in AICc (Δ AICc) values for mixed effects regression models of the effect of sex (female, male), season (open, ice), and diel period (day, night) on movement rate (mvmrt) of 39 Burbot in Bad Medicine Lake, Minnesota, between May 2019 and September 2020. Individual differences were included as a random factor in all models (fish.id).

Model	**AICc**	**Δ AICc**
mvmrt ∼(1 | fish.id) + sex * diel * season	5,155,054	-
mvmrt ∼(1 | fish.id) + season * diel	5,155,802	749
mvmrt ∼(1 | fish.id) + sex * diel	5,156,057	1,003
mvmrt ∼(1 | fish.id) + sex + diel + season	5,156,344	1,291
mvmrt ∼(1 | fish.id) + season + diel	5,156,349	1,296
mvmrt ∼(1 | fish.id) + sex + diel	5,156,383	1,329
mvmrt ∼(1 | fish.id) + diel	5,156,387	1,334
mvmrt ∼(1 | fish.id) + sex * season	5,171,650	16,597
mvmrt ∼(1 | fish.id) + sex + season	5,171,953	16,899
mvmrt ∼(1 | fish.id) + season	5,171,957	16,904
mvmrt ∼(1 | fish.id) + sex	5,171,993	16,940
mvmrt ∼(1 | fish.id)	5,171,998	16,944

Table 4

Small-sample corrected Akaike information criterion (AICc) values and difference in AICc (Δ AICc) values for mixed effects regression models of the effect of sex (female, male), season (open, ice), and diel period (day, night) on turning angle (angle.abs) of 39 Burbot in Bad Medicine Lake, Minnesota, between May 2019 and September 2020. Individual differences were included as a random factor in all models (fish.id).

Model	**AICc**	**Δ AICc**
angle.abs ~(1 | fish.id) + sex*diel*season	4,101,454	-
angle.abs ~(1 | fish.id) + season*diel	4,101,672	218
angle.abs ~(1 | fish.id) + sex + diel + season	4,102,907	1,453
angle.abs ~(1 | fish.id) + season + diel	4,102,911	1,457
angle.abs ~(1 | fish.id) + sex*season	4,103,693	2,239
angle.abs ~(1 | fish.id) + sex + season	4,103,768	2,314
angle.abs ~(1 | fish.id) + season	4,103,772	2,317
angle.abs ~(1 | fish.id) + sex*diel	4,106,883	5,429
angle.abs ~(1 | fish.id) + sex + diel	4,107,015	5,560
angle.abs ~(1 | fish.id) + diel	4,107,018	5,5643
angle.abs ~(1 | fish.id) + sex	4,107,882	6,428
angle.abs ~(1 | fish.id)	4,107,885	6431

Figures

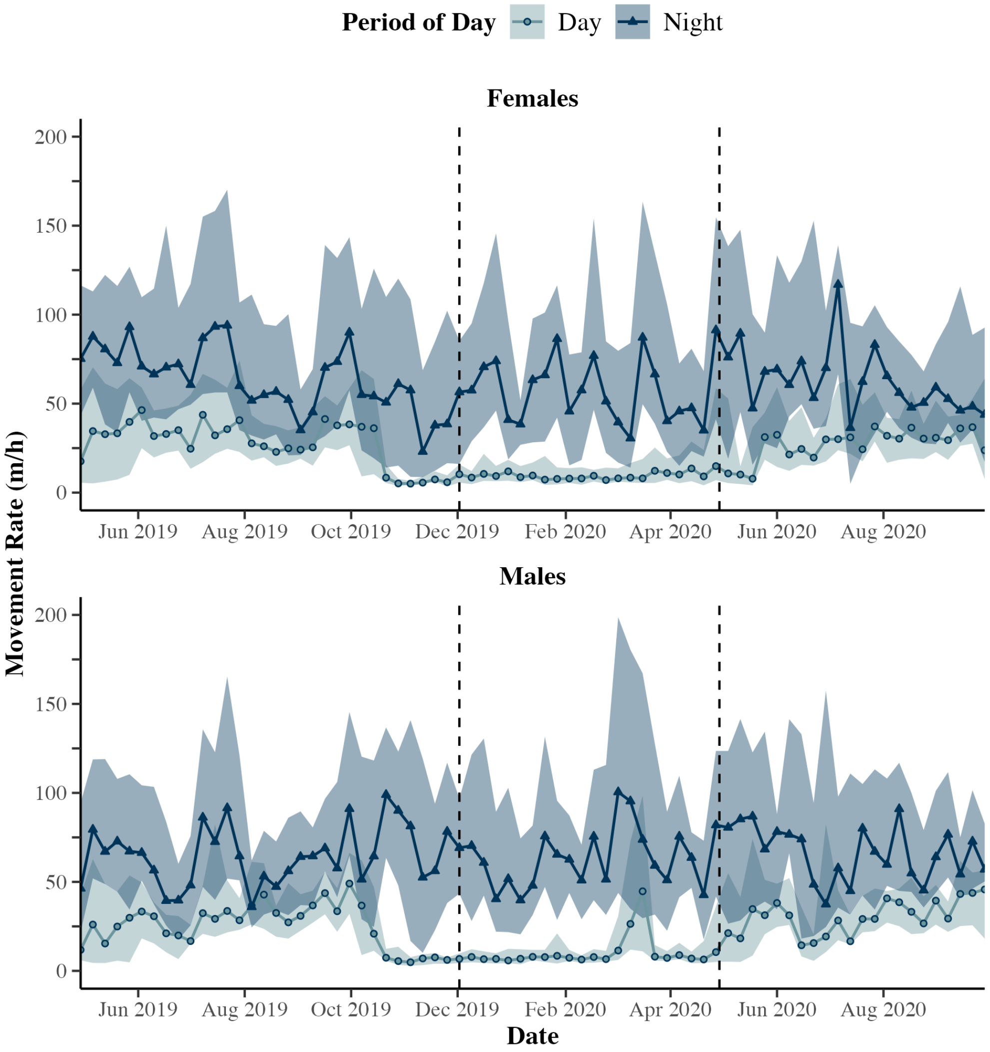

Figure 1

Weekly median movement rates (m/h) for (a) females and (b) males of 39 Burbot in Bad Medicine Lake, Minnesota, between May 2019 and September 2020. Weekly median and interquartile range (IQR) were calculated using the daily median movement rate for each individual during day (light blue circles) and night (dark blue triangle). Points represent median and shaded regions display IQR. Dashed lines indicate ice-on in December 2019 and ice-off in April 2020.

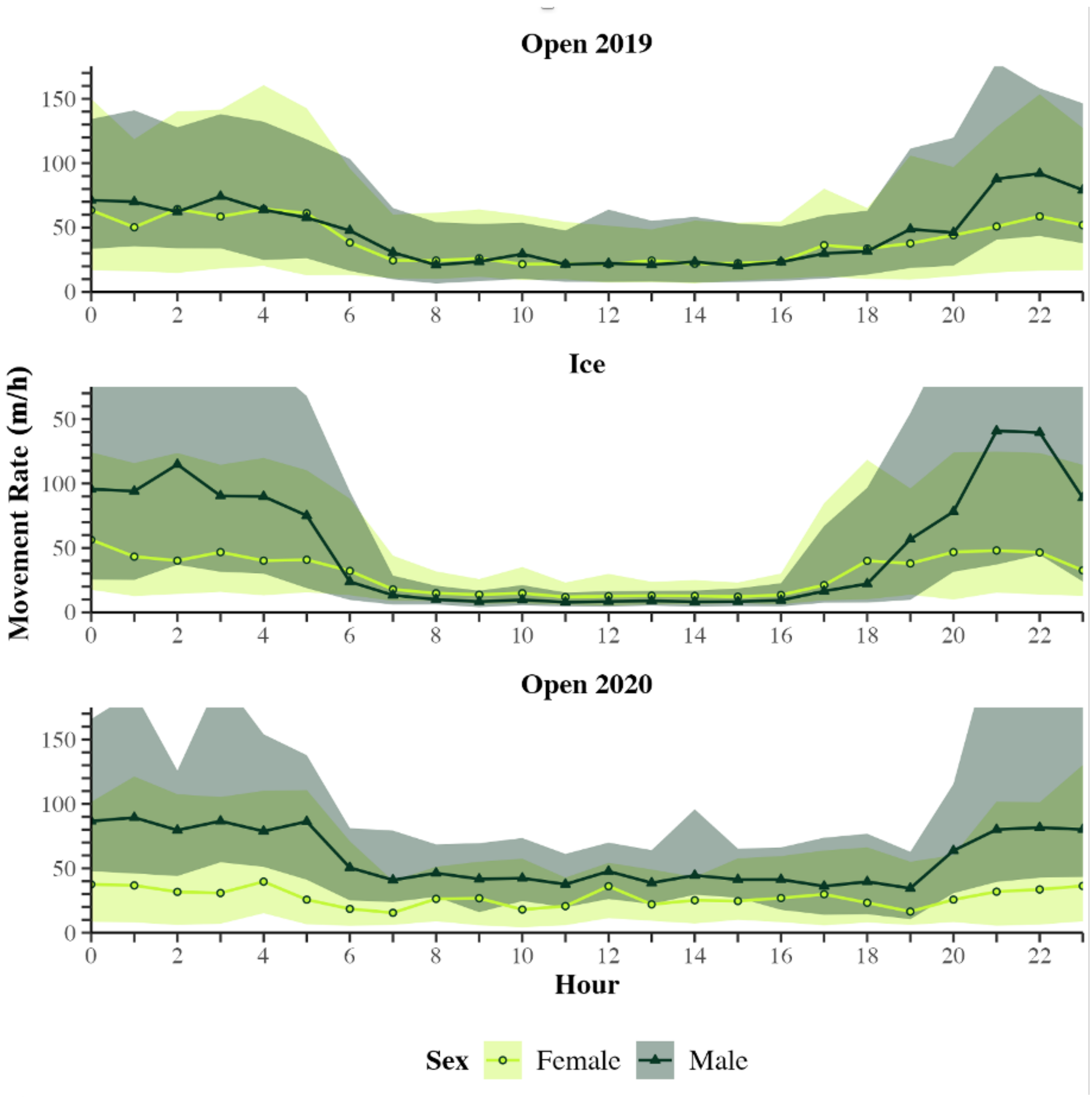

Figure 2

Median movement rate (m/h), by hour, of 39 Burbot in Bad Medicine Lake, Minnesota, between May 2019 and September 2020, across three temporal periods, including open water in 2019 (Open 2019), the ice-covered period between 2019 and 2020 (Ice On), and the open water in 2020 (Open 2020). Movement data are reported for both females (light green circles) and males (dark green triangles). Median and interquartile range (IQR) were calculated using the hourly median movement rate for each individual. Points represent median and shaded regions display IQR.

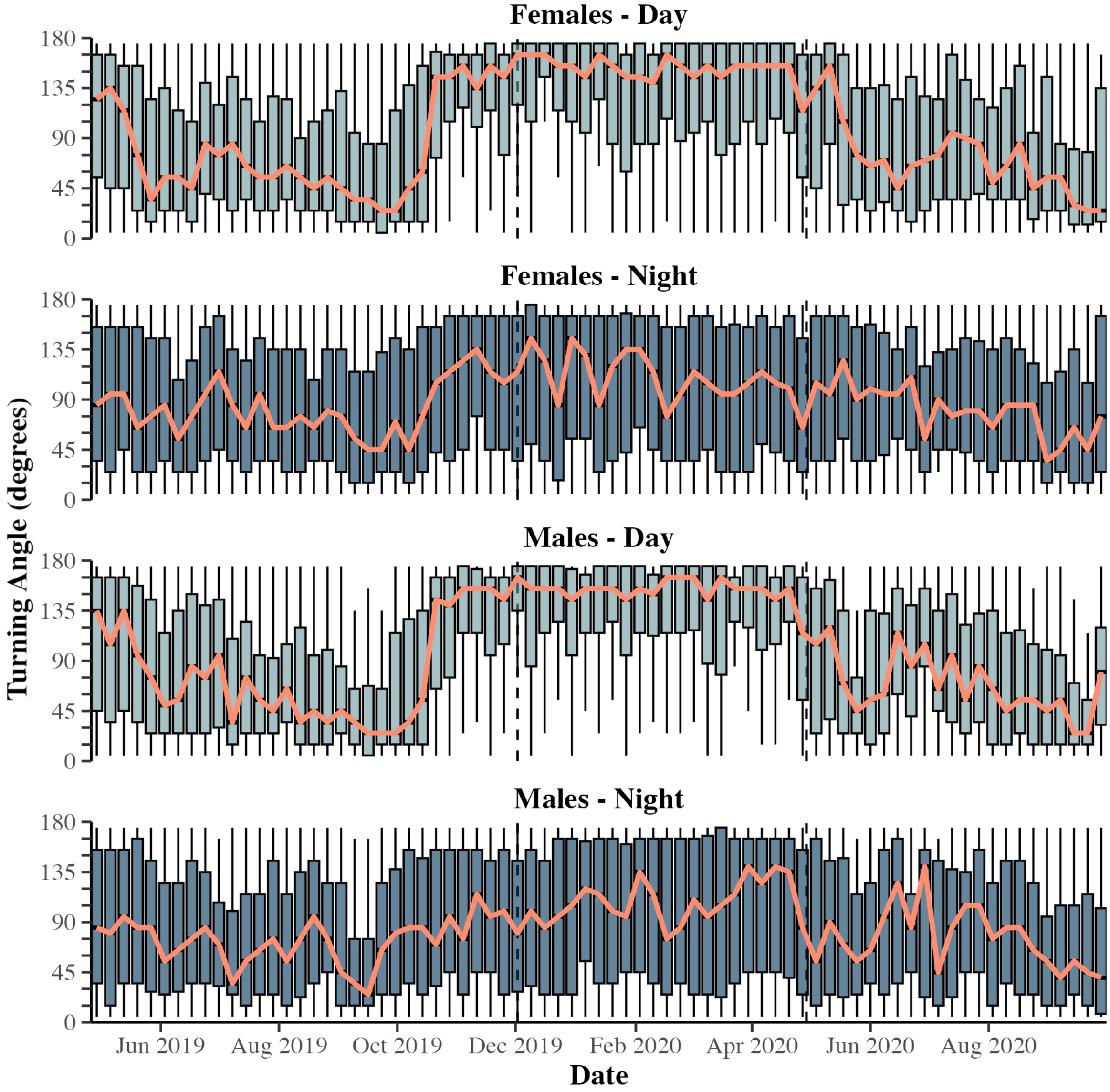

Figure 3

Weekly median turning angle (degrees) for females and males of 39 Burbot in Bad Medicine Lake, Minnesota, between May 2019 and September 2020. Weekly median and interquartile range (IQR) were calculated using the daily mode of turning angle for each individual, using 10° bins. Boxplots represent the IQR of modes, by week, and the orange line shows weekly median over time. Data are reported for day (light blue) and night (dark blue). Dashed lines indicate ice-on in December 2019 and ice-off in April 2020.

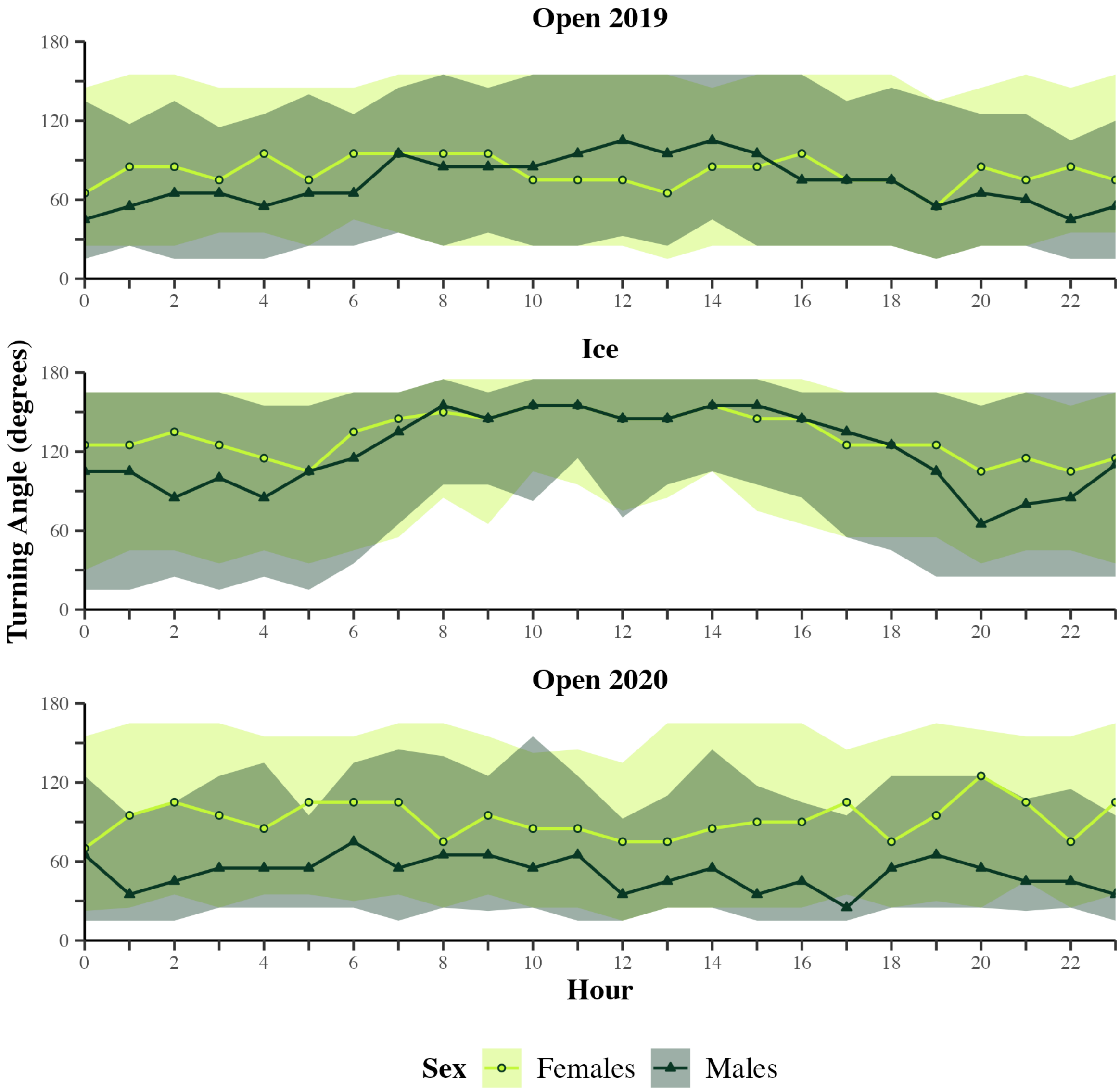

Figure 4

Turning angle (degrees) by hour of 39 Burbot in Bad Medicine Lake, Minnesota, between May 2019 and September 2020, across three temporal periods, including open water in 2019 (Open 2019), the ice-covered period between 2019 and 2020 (Ice On), and the open water in 2020 (Open 2020). Movement data are reported for both females (light green circles) and males (dark green triangles). Median and interquartile range (IQR) were calculated using the mode of turning angle for all individuals. Mode was calculated for each individual, by hour, using turning angle binned by 10 degrees. Points represent median and shaded regions display IQR.

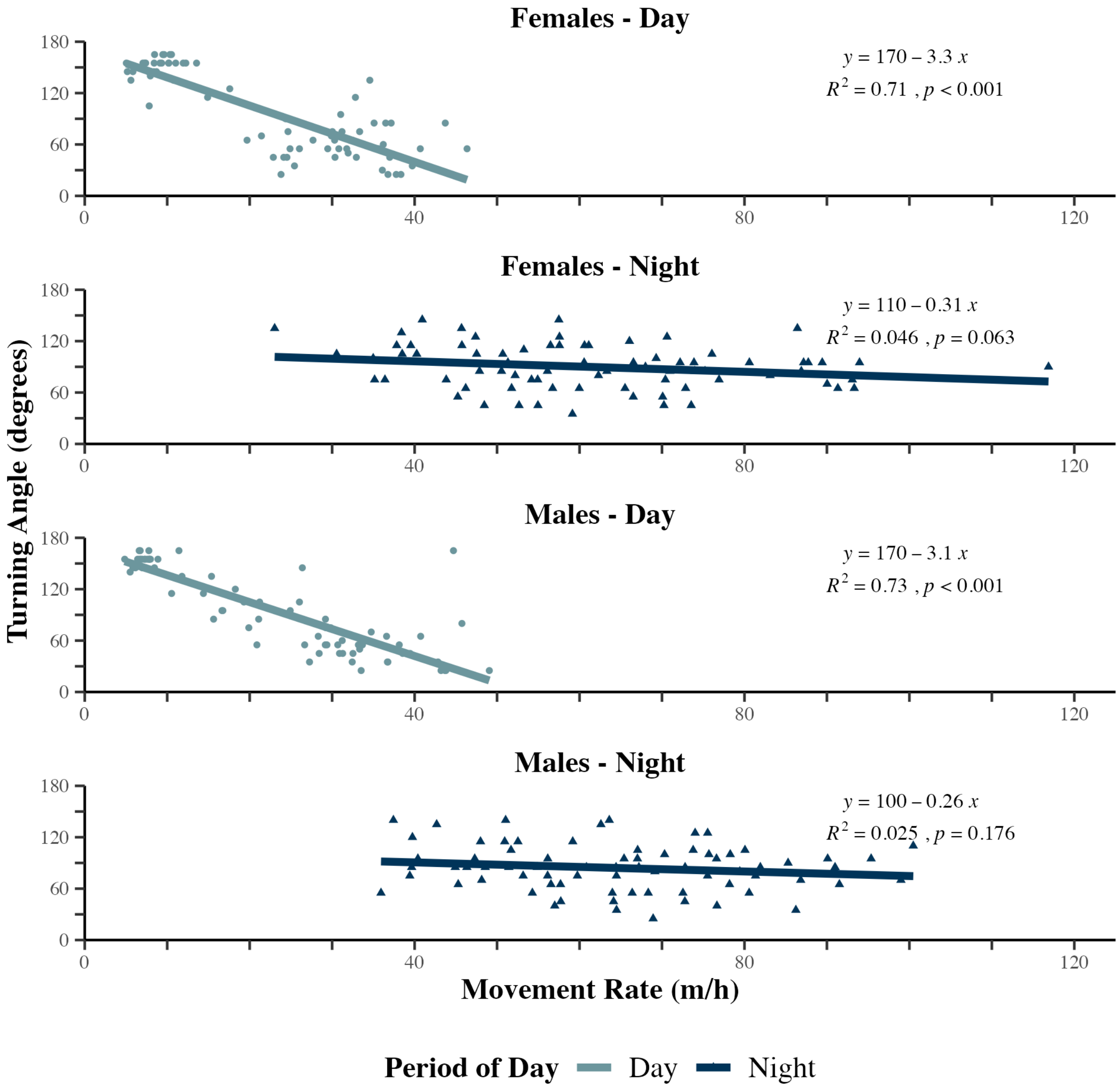

Figure 5

Median turning angle (degrees) was plotted against median movement rate (m/h) for females and males during day (light blue circles) and night (dark blue triangles). Weekly medians were calculated using the daily median of each individual. Each point represents one week. Lines represent linear regression models for the effect of median movement rate on median turning angle. For daytime, 71% of variation in median turning angle of females ($p < 0.001$) and 73% of variation in median turning angle of males ($p < 0.001$) were explained by median movement rate.