

A DESCRIPTION OF RELATIONAL PATTERNS OF MOVEMENT DURING 'RITUALIZED FIGHTING' IN WOLVES

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Abstract. Schenkel (1947, 1967) was the first to describe 'ritualized fighting' in wolves. The current study identifies a set of movement patterns employed during such interactions. The relations between the interactants' movements and the contribution of each individual to these relations are emphasized. Three relational variables are employed to describe interactions: relative distance, relative orientation, and the points of opposition between the interactants. These variables in combination form a three-dimensional interaction space in which a single point describes the momentary state of the configuration of the wolves. The maintenance of four relative configurations plus five transitions between such configurations comprised a consistent set of behavioural patterns. These regular patterns of relational movements indicate that each interactant's movements are constrained in part by a set of rules related to the simultaneous movements of the social partner. In addition, the description of the actual movements in the environment by the individual interactants revealed role-dependent individual contributions by the two interactants to the coordination and management of the relational variables.

The rich and flexible social behaviour of wolves was described first by Schenkel (1947). Schenkel concluded that any representation of interactions as unitary patterns performed by single animals, one at a time, was not adequate. He described combinations of behavioural components, each having potential significance of its own. Components such as torso posture, head and neck position, tail movement, ear position, and facial expression combine to produce a vast number of whole-animal configurations. Schenkel also stressed that further complications were introduced when it became necessary to consider configurations which involved both animals rather than just one interactant. He concluded that the variety and relational nature of the movement of interacting wolves, particularly in what he called 'ritualized fighting' (Schenkel 1967), necessitated a conceptual and analytic framework not available at the time. Much of the detail of such interactions has remained resistant to rigorous analysis (see Mech 1970; Fentress et al. 1978; Moran & Fentress 1979 for reviews). The current study examines 'ritualized fighting' in wolves and identifies easily recognizable movement patterns employed during these interactions.

Schenkel's description of wolf social behaviour was useful as a first approximation. The absence of an adequate descriptive language, however,

led him to confound functional, inferred motivational, and formal criteria. Threat, inhibited bite, and tail-up were used simultaneously to describe a behavioural configuration, for example. Numerous authors (see Hinde 1970; Golani 1976; Purton 1978; Moran & Fentress 1979) have suggested that ethologists should first confine themselves to one of these levels at a time, and only then study their interrelations.

The failure to separate questions of function, cause, and form is but one source of confusion in the description of behaviour. Quantitatively oriented ethologists often restrict themselves to categories of behaviour based on form, yet these categories are defined implicitly by combinations of criteria taken from a variety of variables and frames of reference. Ear position might be described relative to the animal's own body; an approach defined according to the distance between interactants; orientation relative to the social partner; tail position relative to gravity; and, head movements in terms of their relation to a second animal. The significance of such variables, and the existence of ordered relations between them, represent hypotheses that can not be assumed from the outset. Two interacting wolves might continuously manage the distance between them, their relative orientation, and the part of their body nearest the social partner. These variables can be recorded at the same time, but independently of one another. One can then examine their interrelations for regularity of position or movement (see Golani et al. 1979).

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In the present study seven variables were recorded continuously. Four variables describe the behaviour of individual wolves in the environment: changes of orientation and the actual progression of each. The other three variables describe relations between the movement of two wolves. These variables are the distance separating the interactants, their relative orientation, and the body part nearest the partner.

Relative distance during social encounters was first studied systematically by Hediger (1950), who introduced the concepts of individual space and flight distance. Points of opposition between interactants were studied in Tasmanian devils and golden jackals by Golani (1976). He found that these mammals frequently formed fixed contact points with each other. The interactants move in a coordinated fashion seemingly to maintain these points. Contact pathways from one such relatively stable contact point to another were shown to proceed along specific trajectories.

These studies examined relative distance and opposition in isolation. The current study adds the variable of relative orientation and examines the interrelations between the three. The three relational variables in combination define all possible dynamic and static configurations. They define a theoretical interaction space. What part of this space is actually employed during an interaction and in what fashion are subjects of this study. Furthermore, the study shows how the relational variables are managed and coordinated through the employment of specific role-dependent individual contributions by the two interactants.

Method

Study Areas and Subjects

All subjects were members of a captive group of wolves (*Canis lupus*) composed of six females and two males. Observations were made in a wooded research compound, 195 m × 195 m, in the Nova Scotia Wildlife Sanctuary near Shubenacadie, N.S. (45° lat., 64° long.). The animals ranged in age from 1 to 5 years at the beginning of the study in the spring of 1975. Two animals were sisters born in 1973 (Suzie and Sally) but unrelated to the other members of the group. The remaining animals were an older female born in 1969 (Zelda) and members of a litter born in the spring of 1974 (Thor, Milford, Kluane, Juniper, Grey). Identification of individuals was possible using cues provided by distinctive body shapes, coat colours, and

markings. The wolves were fed three to five times per week. Each animal received approximately 55 kg of chicken and 11 kg of Purina Dog Chow per week. Vitamycin vitamin and mineral supplement was provided regularly. All filming and observations were made from a trailer located adjacent to a large clearing at the front of the compound. The trailer was equipped with a large window for observations and a camera slot for filming.

Data Collection Procedure, the Interaction, and the Interactants

Data and film collected from June 1975 until February 1977 are discussed in this study. Observations were taken between three and five times per week in the early morning or at dusk. The 21-month study period included 612 h of data recording on 256 days, each involving at least 1.5 h of continuous observation. Observations were recorded on tape for transcription and classification. Each observation period began with the provision of food for the wolves in a single pile near the centre of the observation area. Activity during observations did not centre around the food, however. Food seemed to act as a catalyst-like event for a period of social activity in the observation area. All members of the group spent a large proportion of the observation period in view and engaged in a variety of activities ranging from solitary resting and investigation to active social interaction in pairs and groups.

The study included two components which occurred concurrently: the description and analysis of social relationships in the group and the filming of specific interactions for detailed analysis of movement. The analysis of social relationships will be presented elsewhere. An interaction was defined as a period during which the movements of two animals were judged to be reciprocally influenced following an approach by one of the interactants. Analysis for the present paper was performed on one of the classes of interaction that was observed frequently throughout the study and was called 'supplanting'. The wolf making the initial approach was designated the Supplanter (S). The second interactant was referred to as the Displaced Animal (D). In all supplanting interactions, D moved away from the direction of an approach by S. This class was further subdivided into those interactions that ended with the withdrawal of D (simple supplantings) and those interactions that featured a period of interaction

following the initial approach and withdrawal. This latter group, called 'extended supplantings', was suited particularly well for detailed movement analysis. Extended supplantings featured the greatest amount of movement. These interactions were shown only by animals that had well-established relationships and resemble interactions described by Schenkel (1967) as 'ritualized fighting'. Regular and high-quality film records of these interactions could be made, and conclusions derived from film could be evaluated in the larger sample available through real-time observations.

Supplanting interactions comprise an important component of wolf social behaviour. They accounted for fully 75% (2102 of 2823) of all interactions observed. Two pairs of animals, Zelda-Sally and Zelda-Suzie, accounted for the majority (66%) of supplantings. Zelda maintained consistent and similar relationships with Suzie and Sally throughout the first 18 months of the study. Supplantings were initiated only by Zelda during this period. These two relationships were distinguished further because extended supplantings consistently made up a substantial proportion of their interactions: Zelda/Suzie, 45% (327 of 700); Zelda/Sally, 34% (233 of 685). No other pairs regularly displayed extended supplanting interactions: all other pairs, 8% (60 of 709). Only interactions between Zelda and Suzie and Zelda and Sally were used in the analysis presented in this paper. The data from both pairs and for interactions recorded during various periods of the study were pooled for analysis. References to the S are to Zelda and to the D are to Suzie or Sally.

The Analysis of Social Movement

The Eshkol-Wachmann (E-W) Movement Notation system (see Eshkol & Wachmann 1958; Eshkol 1973; Golani 1976; Golani et al. 1979) was used extensively for movement analysis during this study. Mention of a few of the E-W system's more pertinent features will serve as an introduction to the analytic perspective employed here.

Movement is an ambiguous phenomenon. The temporal and spatial structure of a given movement is as much dependent upon the frame of reference from which it is described as is the speed of a passing train. This notion takes on particular importance in the description of movement during social interactions. One animal's movements may appear very different from the perspective of the social partner than

from the viewpoint of a stationary observer. It is important therefore that the description of movement not be limited to a single intuitively obvious or convenient frame of reference. Alternative descriptions permit the pursuit of behavioural organization and explanations that may not be apparent from a single perspective. A single movement may be described in various frames of reference in the notation system.

Movement is described most often in the absolute frame of reference. In studies of social behaviour, each interactant's movements typically are described independently of those of a partner within a coordinate system defined by a fixed axis in the environment (e.g. the line of sight of the observer). The behavioural regularities of each interactant then must be recombined to search for relations between the behaviour of two animals. It is possible to search directly for relational movement patterns using the E-W system by describing the interactions within a relational frame of reference. In this frame of reference the descriptive coordinates are defined by the momentary position of the social partner. The changes in orientation of the longitudinal axis of one interactant, for example, are described relative to the longitudinal axis of the partner. Movements and positions are then not simply descriptive of one animal, but measure the behaviour of both interactants.

Individual interaction sequences were described using the E-W system. Thirty complete sequences were notated during this initial phase. The highest-quality sequences were essential to this initial search for regularities in the movements of the interactants. Therefore, rather than using a statistical selection procedure, the best film sequences were used to formulate informal hypotheses, which were later evaluated using the larger sample of filmed interactions and real-time observations. (A total of 66 rolls or 3 h and 18 min of film were collected. Sixty-eight supplanting interactions between Zelda and Suzie and 76 between Zelda and Sally were filmed.) Various aspects of movement were described initially; regularities were identified in particular sequences; and further sequences then were examined to determine the generality of these patterns. The limits of regularities were refined on the basis of emerging consistencies and variations between samples. Ultimately a comprehensive picture of the organization of movement in these interactions emerged. Aspects of the behavioural organization could then be examined in detail by using graphic representations. Com-

plete sequences of interaction were later examined to determine if the system of classification could account for the range of movement observed in full interactions. Once the elements of the system had been identified using frame-by-frame film analysis, it was possible to recognize these elements in real-time observations; something that was not possible before. The compatibility of the system of organization with movement in interactions that were observed and described in detail but not filmed could then be assessed.

Three independent relational variables and two variables describing the movement of each individual were employed throughout this study. The relational variables were:

(1) **Relative distance.** Relative distance was measured by notating the distance between the two interactants. 'Wolf-length' (excluding tail) was used as the unit of measure because it vividly conveyed this aspect of the interaction and eliminated the problems associated with estimating a metric unit of distance from interactions filmed at various distances from the camera.

(2) **Relative orientation.** The orientation of each animal was described relative to the simultaneous orientation of the social partner. This variable was measured using a set of compass-like coordinates zeroed by the longitudinal axis of the second wolf in the interaction. Changes in this variable could be the result of movements by either animal or both animals simultaneously.

(3) **Point of opposition.** Point of opposition was used to indicate the point on each animal's body to which the social partner was nearest. Opposition need not imply physical contact between the interactants. The distance between the interactants was notated separately. Changes in point of opposition can be produced by movements of either or both animals. A single change in opposition might be the result of a number of distinct combinations of movements by the interactants.

The variables describing movement of each individual were:

(1) **Shift of front.** Shift of front is used to describe turning of the animal in the environment. The 'front' of the animals was defined by the longitudinal axis of the wolf drawn perpendicular to the shoulders.

(2) **Progression.** Progression refers to actual movement of the body in the environment, usually by walking or running. Progression de-

notes movement in the direction of the front of the animal unless otherwise specified.

A temporal degree of resolution of 6 frames or 0.25 s was used throughout.

A three-dimensional 'interaction space' was created using the three variables as illustrated in Fig. 1. A single set of three values within this space is represented by a point. Each point specifies an instantaneous social configuration from the point of view of one of the interactants. The space includes all theoretically possible social configurations. A trajectory through interaction space is obtained by following successively the three-dimensional points recorded during an interaction. This trajectory provides a dynamic reconstruction of the interaction.

Golani (1976) coined the term 'kinetic field' to describe the network of pathways along which the two animals move around one another during an interaction. The trajectories in the interaction space employed in this study trace out a three-dimensional kinetic field. Identifying the rules of movement in extended supplanting interactions can then be translated into the search for the organization of the kinetic field in the interaction space. The interaction space should be seen not only as an abstract representation of the interaction, but also as an aid to

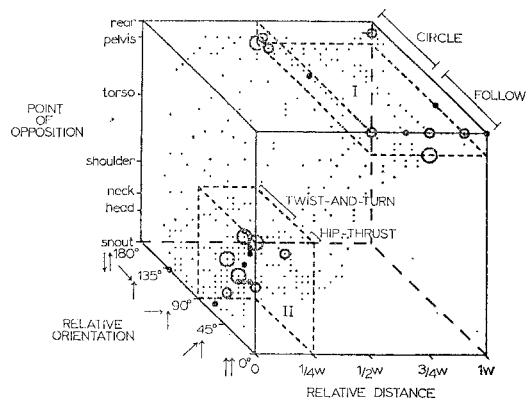


Fig. 1. The interaction space composed of the three relational variables used in the description of movement during extended supplantings. Three complete extended supplantings are plotted in the interaction space. Each point represents values of the three relational variables taken from every second frame of film at 24 frames per second. Successively repeated observations are indicated by an incremented size of plotted points: small point, 1-2; large dot, 3-10; small circle, 11-25; large circle, more than 25 observations. Boxes indicate region I (upper right) and II (lower left). Approximate range of configurations associated with each of four types of stable configurations are indicated.

visualizing the actual movements of the interactants.

Relational descriptions are presented for D throughout this paper. The complementary values for S are provided only where they are not redundant.

Results

In all extended supplantings S and D exhibited consistent and distinctive positions of various body parts. These distinctions are illustrated in Fig. 2. S exhibits erect ears turned toward the front of the head; whereas D holds the ears flat against the head and turned to the rear. The tail of S is held at back level or above in contrast to that of D which lies between the rear legs and against the animal's underbelly. S exhibits a digitigrade stance with hind legs fully extended, while D holds the hind legs relatively flexed and walks and stands in a somewhat plantigrade fashion. These postural distinctions were observed in all extended and simple supplantings. Some individuals exhibited the characteristics of D in one relationship and those of S in another.

Two broad classes of regularities emerged from the description of movement using the three relational variables: (1) movements of both animals that combined to hold a configuration relatively constant, and (2) movements that resulted in a change of configuration. The former relational patterns are referred to as 'relatively stable configurations' and the latter patterns are called 'transitions'.

Three complete interaction sequences are plotted in the interaction space presented in Fig. 1. Relative distance, orientation, and opposition were recorded for every second frame of film (24 fps, 1956 frames). The uneven distribution of points indicates that the animals did

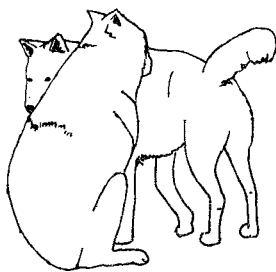


Fig. 2. An artist's illustration of the Stand-Across position showing the static postural distinctions between Supplanter (S) and Displaced Animal (D) (see text for detailed description).

not assume certain ranges of configurations during these interactions. The absence of points in the lower right of the space, for instance, indicates that when the animals were separated by more than one wolf-length the hindquarters were the closest part of D's body to S. The relatively large number of points in the lower left portion indicates that when the animals were close to one another, it was the forequarters rather than the rear portion of D that was closest to S.

In this illustration two distinct portions of the interaction space were utilized most: the upper right front and the lower left. The distribution of the larger symbols in Fig. 1 indicates that sets of relative values were maintained only in these two regions. The upper right region represents stable configurations where the animals were separated by more than half a wolf-length and where the forepart of S was closest to the hindquarters of D. Points in the lower left front region represent maintenance of contact or near-contact between the forequarters of the interactants in a relative orientation between parallel and 90°. These two broad ranges of the interaction space were labelled regions I and II respectively, distinct and exclusive portions of the interaction space in which relatively stable configurations occurred. Although the sequences in Fig. 1 serve first as illustration, no stable configurations other than those included in the two regions were observed during the study.

Notation of 30 complete sequences of extended supplants, examination of 143 filmed sequences, and real-time observation of 620 other interactions did not reveal any configurations that were maintained other than those described below. Points at other portions of the interaction space represent transient social configurations through which the interactants passed as they shifted from one maintained configuration to another.

Relatively Stable Configurations

Configurations were maintained principally by simultaneous compensatory movements rather than by the assumption of static postures by both interactants. It was possible to classify the stable configurations into four qualitatively distinct types, two within region I of the interaction space and two within region II.

The identification of these four configurations, as well as all other relational patterns described in this paper, was based on multiple viewing of film records while reading notation scores. Nevertheless, once specified but not before, all

patterns could be readily identified by a relatively untrained observer during real-time observations.

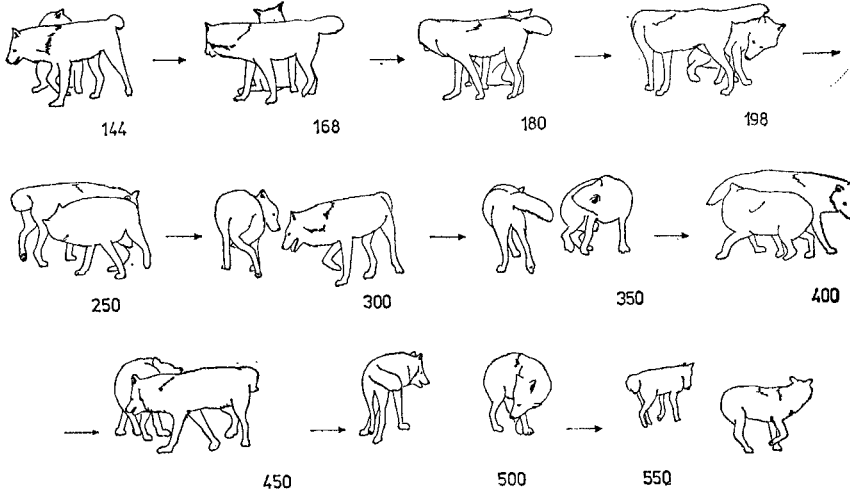
Of the 240 stable configurations recorded on film, 121 occurred in region I. These configurations fell within two non-overlapping subregions with different ranges of relative orientation. As indicated in Fig. 1, one type of configuration is nearly anti-parallel. This type was labelled

Circling. In the second the interactants are parallel or near-parallel and S follows D. This type was called Following.

1. Circling

Relational structure. An artist's illustration of Circling is presented in Fig. 3a, frames 198-500. The interactants move slowly in a slightly off-

a. CIRCLING



b. FOLLOWING

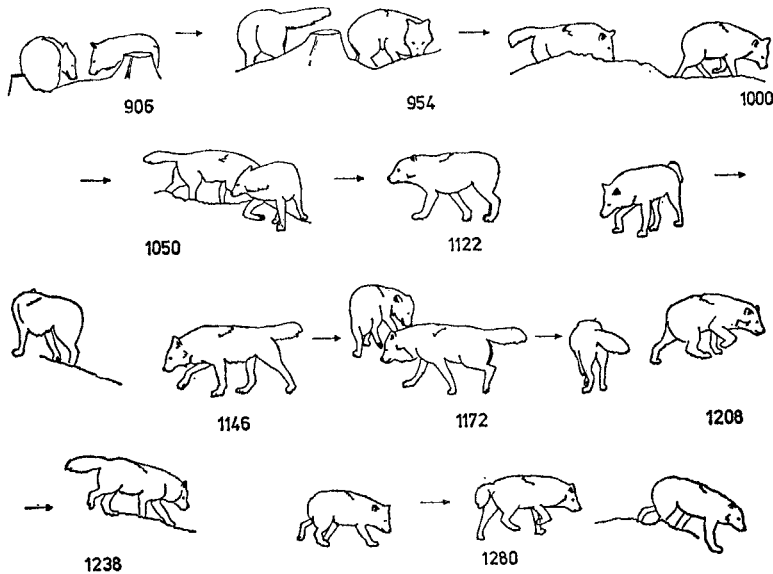


Fig. 3. An artist's illustration of a Circling and Following. Numerals represent frame numbers (24 fps).

anti-parallel orientation; the head of S is closest to the hindquarters of D, separated by at least half a wolf-length. Note the clear postural features of each interactant described earlier. Small fluctuations of one or more of the relational variables are interspersed with periods of actual maintenance of all three variables. The relational patterns were called relatively stable configurations for this reason.

Records of the three relational variables during four examples of Circling are presented in Fig. 4a. In examples 3 and 4, the Circling pattern does not begin until the point of opposition reaches the 'rear' value on D. Distance and relative orientation are maintained for a period of time and then shift to new values, which are again maintained. In all four examples relational values are maintained with relatively small fluctuations and are limited to region I. Inter-animal distance is held at half a wolf-length or just above; the pair maintains a near anti-parallel relative orientation; and opposition is held steadily at the rear of D.

Individual contributions. Figure 5a illustrates the contributions of S and D to the maintenance of a typical Circling configuration. Both interactants shift front continuously and at the same time progress forward minimally. This combination of individual movements is unique among relatively stable configurations.

2. Following

Relational structure. Figure 3b reveals that during Following, opposition is between the head region of S and the rear of D and the interactants are separated by at least half a wolf-length. A relative orientation near parallel is maintained for most of the sequence.

Fluctuations of the three relational variables during four examples of Following are presented in Fig. 4b. Opposition is maintained with minimal or no variation. Both relative distance and orientation show greater variations. Following involves extensive movement, and obstacles are ultimately encountered and turns necessitated. Large deviations from parallel often indicate such turns by the two wolves (e.g. example 2). The leading wolf (D) turns; S replicates that turn at the same point in space; and finally, the pair resumes following in parallel. The faithful replication of the path of the leading animal by the second wolf is striking. Such changes of direction can be seen in Fig. 3b (frames 1172–1280). The smaller deviations in relative orientation apparent in example 3 are the product of commonly seen small shifts of front by the leading animal (D), as if to 'look back' at the following wolf. Relative distance is typically maintained steady for short periods of time, and then is shifted to a new maintained value, but these values are always within the range of half a wolf-

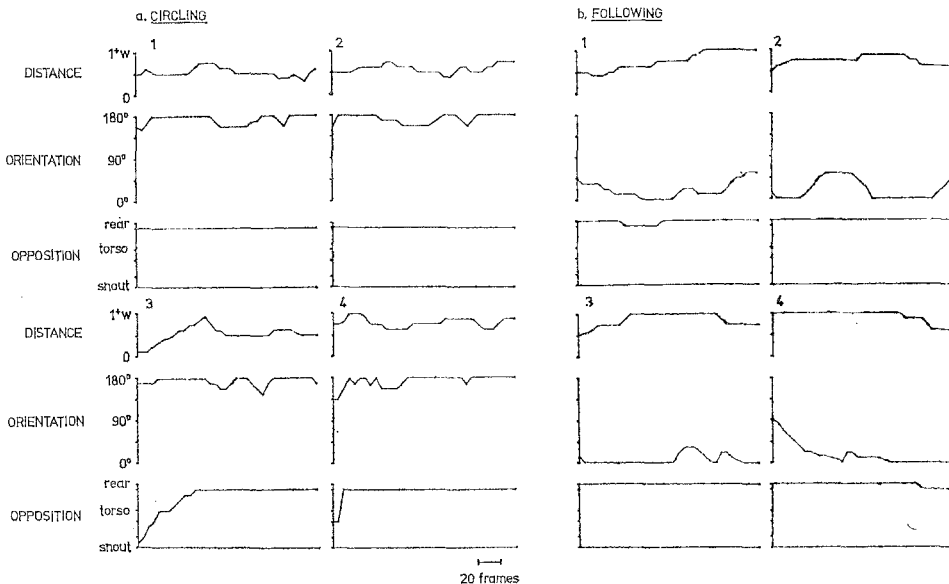


Fig. 4. Changes of the three relational variables during four examples of Circling and Following.

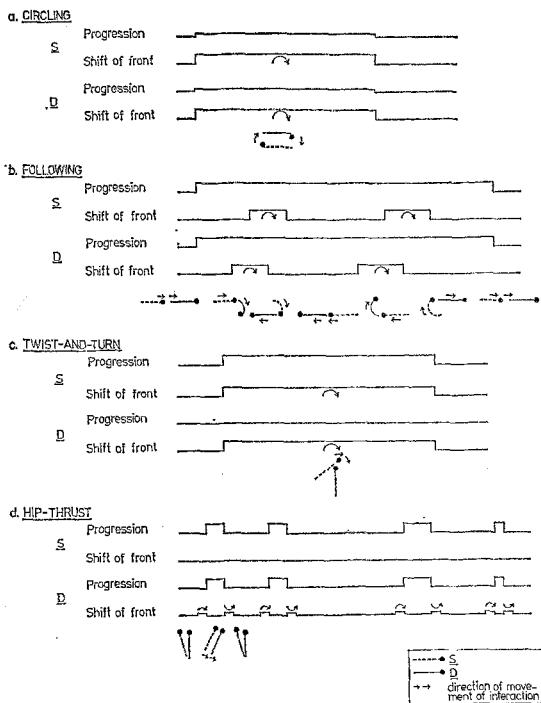


Fig. 5. Movement contribution of each interactant to the four types of stable configurations: (a) Circling; (b) Following; (c) Twist-and-Turn; and (d) Hip-Thrust. For each configuration, shifts of front and progression by each interactant and their temporal relationships are illustrated. A schematic illustration of the configuration is also presented to assist with the interpretation. (Relative distance not drawn to scale.)

length or greater. Relative orientation fluctuates in the range of 0 to 45°; a range distinct from that seen in Circling. Maintained points of opposition are similar in Following and Circling (see Figs 1 and 4).

Following and Circling frequently alternated during an interaction. Although no systematic records of sequence duration were kept, Following tended to be longer than Circling. A particular Following pattern lasted over 30 min, and sequences lasting a minute were common.

Individual contributions. Typical individual movements during Following are shown in Fig. 5b. Following is always maintained by simultaneous forward progression by both interactants. Shifts of front initiated by D are followed closely in time by compensatory shifts of front by S. D is always the leading animal in a Following configuration.

Both Circling and Following fall within the confines of region I as shown in Fig. 1. Stable

configurations in region II feature closer inter-animal distances and often actual physical contact. Points of opposition are maintained more to the front of D than is the case in Circling or Following. Two distinct types of stable configurations could be discriminated on the basis of differences in relative orientation. The Twist-and-Turn featured orientations near 45° to near perpendicular and the Hip-Thrust was maintained at near-parallel orientations. Both these stable configurations were maintained by simultaneous compensatory movements by the interactants. One hundred and nineteen instances of stable configurations in region II were recorded on film.

3. Twist-and-Turn

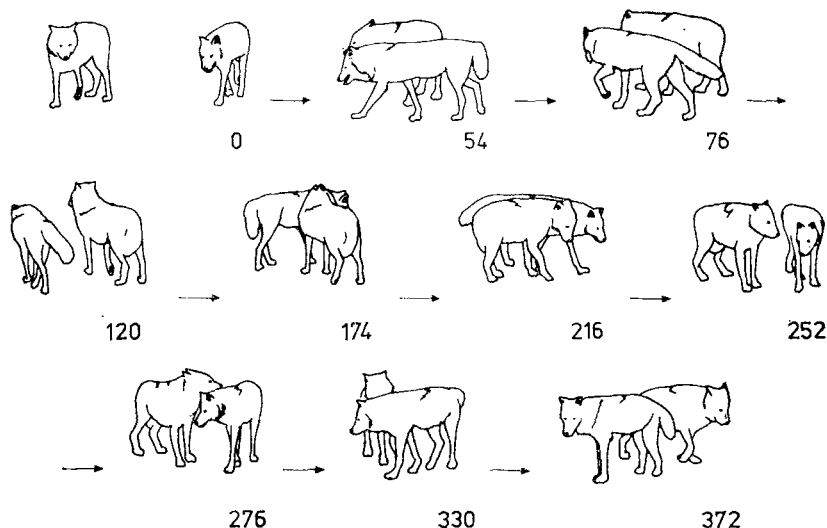
Relational structure. An illustration of the Twist-and-Turn is presented in Fig. 6a, frames 54–330. The pair maintains a relative orientation between near 45° and near perpendicular, with contact, or less than half a wolf-length, between the shoulder area of S and the forepart of D. Maintained points of opposition range only from the shoulder to just back of the shoulder on S and are opposed only to the front and shoulder area of D. Although maintained values of relative orientation are typically near 45° off-parallel, values ranging from near-parallel to near perpendicular sometimes occurred briefly during the Twist-and-Turn (e.g. frames 120 and 174, Fig. 6a).

Four sequences of Twist-and-Turn are illustrated in Fig. 7a. In each example values of both relative distance and point of opposition show little variation. In contrast to the preceding two stable configurations, the animals maintain actual contact or near contact at the shoulder region of D. Relative orientation shows greater variation than either of the other variables, but remains principally near 45°. The performance of this relatively stable configuration features fixations of values of the two former dimensions accompanied by short-term fixations and fluctuations in relative orientation within region II.

The configuration observed during the Twist-and-Turn was frequently maintained without movement by either interactant. The static maintenance was labelled Stand-Across and is illustrated in Fig. 2. In these cases, D was frequently seated.

Individual contributions. Movement roles are apparent from an examination of the Twist-and-Turn represented in Fig. 5c. The top of the 'T' is always formed by S and the base by D. The

a. TWIST-AND-TURN



b. HIP-THRUST

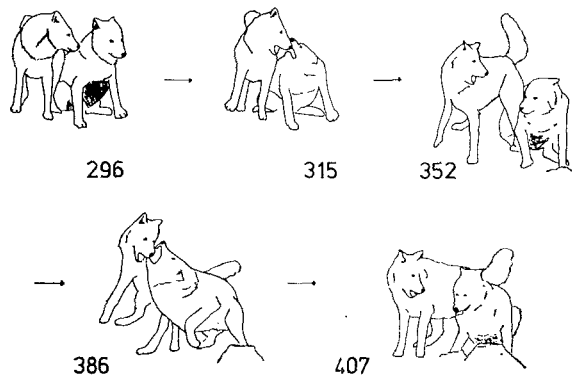


Fig. 6. An artist's illustration of a Twist-and-Turn and a Hip-Thrust. Numbers indicate frame number (24 fps) and a fixed location in the environment.

relational configuration is maintained by both forward progression and shift of front by S and a compensatory shift of front alone by D.

4. Hip-Thrust

Relational structure. Maintained values for the Hip-Thrust are somewhat different from the Twist-and-Turn and the mechanisms of maintenance are quite distinct. Maintenance of the Hip-Thrust configuration is illustrated in frames 315 and 386 in Fig. 6b. It can be seen that the Hip-Thrust features actual physical contact

between the interactants, a near-parallel relative orientation, and points of opposition on both animals slightly to the rear of those maintained during the Twist-and-Turn. Actual thrusting alternates with static configurations, which can be seen in frames 296, 352, and 407 of Fig. 6b. S is turned away from D and the points of opposition on the two interactants are similar to those seen during thrusting.

Figure 7b presents records of the three relational variables for three sequences of Hip-Thrusts. The typical pattern involves simul-

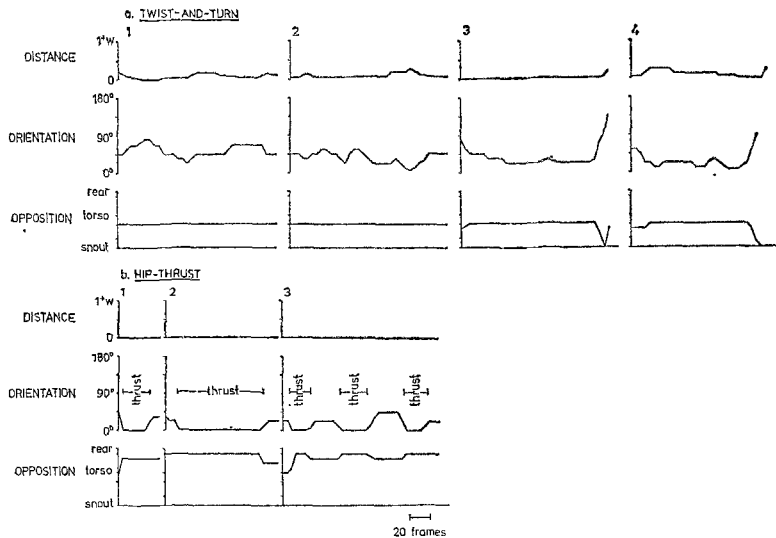


Fig. 7. Changes of the three relational variables during four examples of the Twist-and-Turn and three examples of the Hip-Thrust.

taneous maintenance of values of all three dimensions interspersed with fluctuations in relative orientation. These fluctuations indicate the assumption of the configurations seen in Fig. 6. Thrusts alternate with periods of no movement by either animal.

Individual contributions. The movement contributions to the Hip-Thrust by each interactant are diagrammed in Fig. 5d. A shift of front by D results in a change in relative orientation from off-parallel to parallel (the 'thrust' configuration itself). The return to off-parallel is, similarly, the result of a movement by D alone. The progression during the actual maintenance of the parallel configuration is away from S and toward D. In other words, S is doing the 'thrusting'.

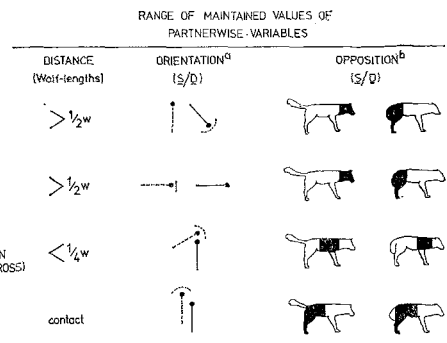
Hip-Thrusts were almost always accompanied by snarling and snapping by both animals near the head and neck regions. The wolves growled loudly, and S frequently displayed vigorous, large tail movements resulting in actual contact with the upper surface of the back of D. Far more baring of the teeth by both interactants was seen during this than in other stable configurations.

5. Summary of Relatively Stable Configurations

Much of the movement exhibited by the two interactants during extended supplantings has the consequence of maintaining a set of three relational variables within relatively narrow

limits. The animals' movements are compensatory (and most often simultaneous), and thus the relative social configuration is maintained. The four distinct types of relatively stable configurations are summarized in Fig. 8. Ranges of values for each variable are indicated. It can be seen that despite some variability for each type, the set of maintained values in each case is distinct from all other stable configurations.

The contribution of each interactant to the maintenance of each stable configuration is consistent. Each interactant displays a distinct



a. Dotted lines represent range of stable orientations.
b. Shaded areas indicate range of stable points of opposition on each interactant.

Fig. 8. Ranges of values of each relational variable observed during stable configurations in the interaction space.

movement role during the maintenance of a particular stable configuration. The speed, direction, and exact amount of each interactant's movement, on the other hand, vary considerably across instances and appear to be constrained primarily by the need to compensate for the movements of the social partner and thus to maintain the configuration.

Although much of the movement of the two interactants contributes to the maintenance of one of these configurations, when examples of interactions were plotted in the interaction space (Fig. 1) points outside of region I and II were observed. These points indicate change of configuration. Transitions from one relatively stable configuration to another are described next.

Transitions in Relative Configuration

Trajectories within the interaction space describe the path of changes in configuration and are called 'transitions.' Transitions involve large changes in some or all of the three relational variables. These changes occur in a regular fashion and were classified into five types on the basis of the direction of the transition and the form of its trace in the interaction space.

1. Swivel/Stand-Across

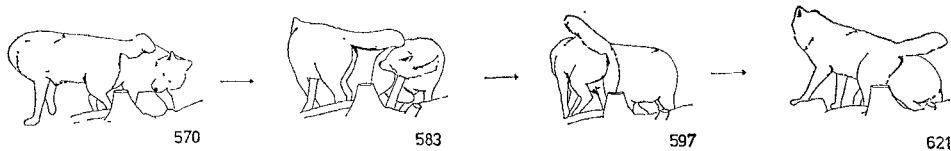
Relational structure. The Swivel/Stand-Across involves a change from a Circling stable con-

figuration in region I to a Twist-and-Turn, Stand-Across, or Hip-Thrust in region II. An artist's illustration of an example of the transition is presented in Fig. 9a. The initial Circling configuration is shown in frame 570 and the final Hip-Thrust in frame 621. The two other illustrations represent momentary configurations from the transition itself.

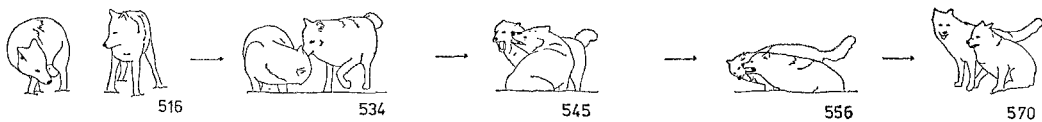
The consistent relational form of the transition can be seen from the examples presented in Fig. 10a. All graphs illustrate the change in relational variables from values in region I to those in region II. Relative distance decreases from more than half a wolf-length to values near zero or actual physical contact; relative orientation changes from anti-parallel to near-parallel; and opposition on D shifts from the extreme rear to the shoulder region. A prototypical trace of the transition is presented in Fig. 11a. It can be seen that the transition moves through the rear portion of the interaction space from region I to region II. The transition is relatively slow.

Individual contributions. The contributions of S and D to the Swivel/Stand-Across are illustrated in Fig. 12a. The transition begins from a Circling configuration. This stable configuration is disturbed by an increase in rate of shift of front by D and the final (Stand-Across) con-

a. SWIVEL/STAND-ACROSS



b. LUNGE/SWIVEL



c. WALK-UP/STOP

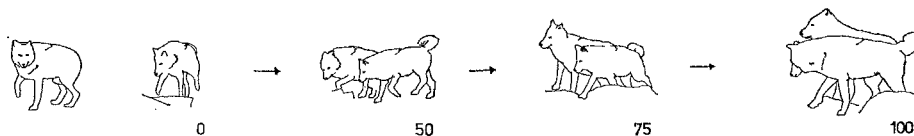


Fig. 9. Artist's illustration of: (a) Swivel/Stand-Across; (b) Lunge/Swivel; and (c) Walk-Up/Stop transitions. Numerals indicate frame number and fixed reference location.

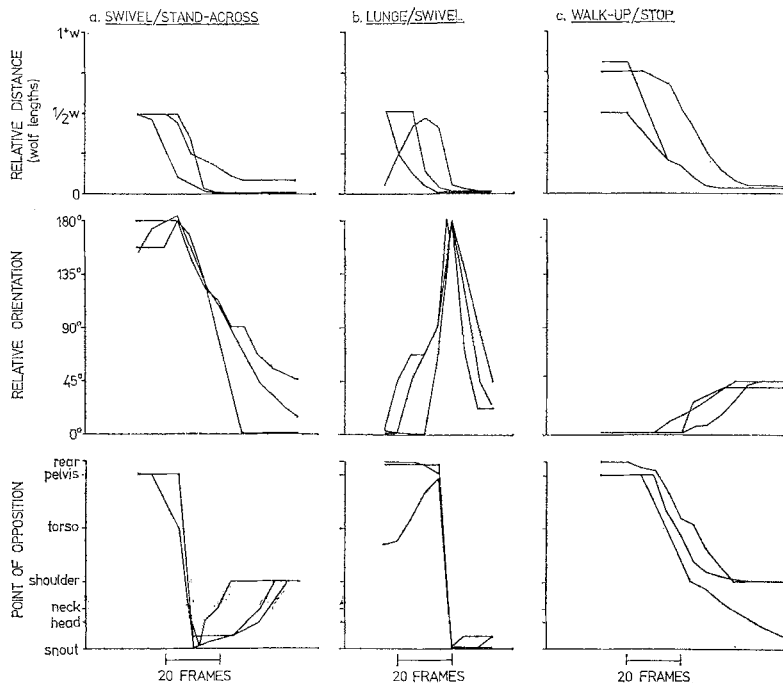


Fig. 10. Changes of the three relational variables during three examples of: (a) Swivel/Stand-Across; (b) Lunge/Swivel; and (c) Walk-up/Stop transitions.

figuration is achieved by a termination of all movement by both interactants or by the resumption of compensatory movements in cases where the transition terminates with a Twist-and-Turn. In either case the transition is accomplished by active movement by D.

2. Lunge/Swivel

Relational structure. The Lunge/Swivel is a transition from the Follow stable configuration in region I to a Twist-and-Turn, Stand-Across, or Hip-Thrust in region II. An example of the transition is presented in Fig. 9b. In this case the initial Follow configuration is shown in frame 516 and the terminal Hip-Thrust in frame 570. The intervening frames illustrate momentary stages of the actual transition.

Records of three examples of the Lunge/Swivel are presented in Fig. 10b. In each case, relative distance decreases to actual contact, orientation shifts through almost 360° and the point of opposition on D moves from the rear to the shoulder area. (In one example both relative distance and opposition increase just prior to the actual Lunge/Swivel. These changes

indicate the completion of another transition to be described shortly.) These changes represent a transition from a Follow to stable configurations in region II as illustrated in Fig. 11b.

Individual contributions. The movement contributions of the two interactants to the Lunge/Swivel transition are diagrammed in Fig. 12b. The initial Follow stable configuration is disturbed by a decrease in rate of progression and a small shift of front by D. As the distance between the two wolves approaches minimal values, D performs a large shift of front of near 360° . Only then does S make any active contribution to the change in configuration, by way of a rapid decrease and termination of forward progression. The ordering and type of movement displayed by each interactant are consistent across examples of the Lunge/Swivel, but duration and amount of movement may vary and shifts of front in both directions are observed.

The Swivel/Stand-Across and Lunge/Swivel are somewhat similar transitions. Both involve a change from stable configurations in region I to those in region II. Both involve the same pattern of change in relative distance and opposition.

They do differ, however, in consistent aspects, which prompted the separate classification used here. The Swivel/Stand-Across is initiated from a Circle and D exhibits a shift of front of about 180°, whereas the Lunge/Swivel always begins from a Follow and involves a 360° shift of front by D. These differences are reflected in a comparison of the trace of the two transitions in the interaction space (see Fig. 11a, b). In addition, the Lunge/Swivel is a faster, more vigorous transition because the larger shift of front by D is performed in a shorter period of time than the smaller shift of front in the Swivel/Stand-Across.

3. Walk-Up/Stop

Relational structure. The Walk-Up/Stop transition is illustrated in Fig. 9c. The transition be-

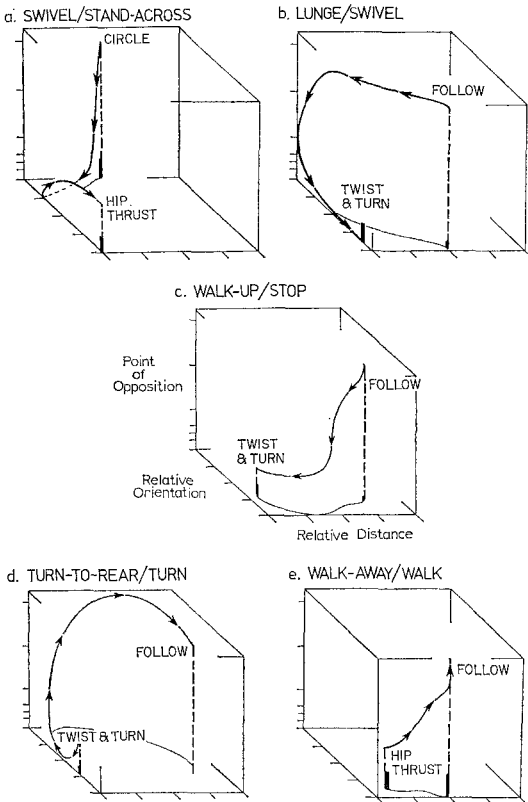
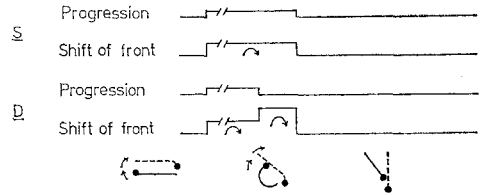


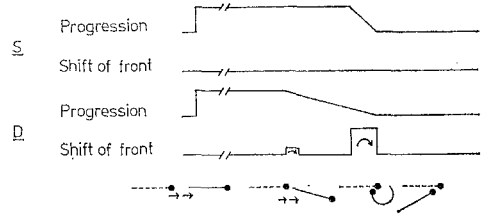
Fig. 11. Prototypical examples of the five transitions represented by the changes of the three relational variables plotted in the interaction space: (a) Swivel/Stand-Across; (b) Lunge/Swivel; (c) Walk-up/Stop; (d) Turn-to-Rear/Turn; (e) Walk-Away/Walk. Arrows indicate direction of relational movement. Incremented base indicates stable configurations preceding and following each transition.

gins from a Follow configuration as shown in frame 0. Between the first and second frame of the illustration, relative distance decreases to near zero. From the second to the third frame,

a. SWIVEL/STAND-ACROSS



b. LUNGE/SWIVEL



c. WALK-UP/STOP

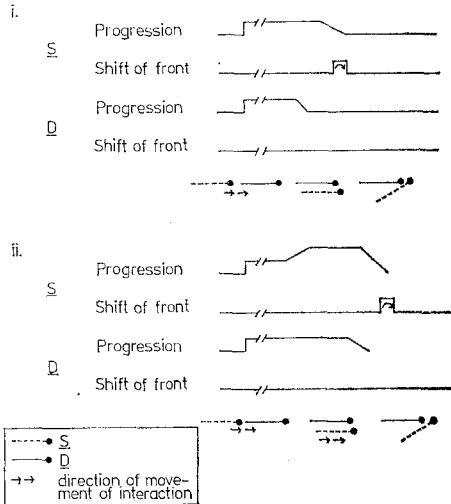


Fig. 12. Movement contribution of each interactant to: (a) Swivel/Stand-Across; (b) Lunge/Swivel; and (c) Walk-Up/Stop. Shifts of front and progressions by each interactant and their temporal relationships are presented for each version of a transition. A schematic illustration of the corresponding relational changes in the interaction produced by these movements by the individuals is presented to assist with the interpretation. (Relative distance not drawn to scale.)

opposition shifts to the shoulder region of both animals, and by the final frame, relative orientation changes to near 45° and the animals assume the Twist-and-Turn stable configuration.

Figure 10c illustrates graphically the smooth transition from a stable configuration in region I to a stable configuration in region II. The patterns of change in each example are similar, as are the relationships between the changes of each variable. The sequence of events illustrated in Fig. 10c of initial decrease in relative distance, change in the point of opposition, and the final change in relative orientation, can readily be seen in each example here. The consistent relation between changes in relational variables is represented by the prototypical trace in the interaction space illustrated in Fig. 11c.

The Walk-Up/Stop contrasts sharply with the Lunge/Swivel and Swivel/Stand-Across. The latter transitions feature large changes in all relational variables, whereas the Walk-Up/Stop leaves the impression of a slow, almost leisurely pattern with relatively small changes in relational variables. All three transitions, however, begin from relatively stable configurations in region I and terminate in stable configurations in region II. Comparison of the traces shown in

Fig. 11 reflects these differences. The Walk-Up/Stop occurs in the front rather than the rear of the interaction space. Unlike the Swivel/Stand-Across and Lunge/Swivel, the Walk-Up/Stop is never followed by a Hip-Thrust.

Individual contributions. The contributions of each interactant to the relational structure of the Walk-Up/Stop are illustrated in Fig. 12c. Two equivalent forms were observed. In the form illustrated in Fig. 12c(i) a Follow is disturbed by a decrease and cessation of forward progression by D. The continued progression by S reduces relative distance and brings points of opposition into the shoulder region and the range of the Twist-and-Turn or Stand-Across configurations. The transition is completed by a small shift of front by S. In the second form of the transition (Fig. 12c(ii)), an increase in rate of forward progression by S precedes the cessation of forward progression by D described above. The two forms are equivalent in that they produce the same relational changes; both in terms of end points and form in the interaction space. S shows no systematic tendency to stand on one side or the other of D.

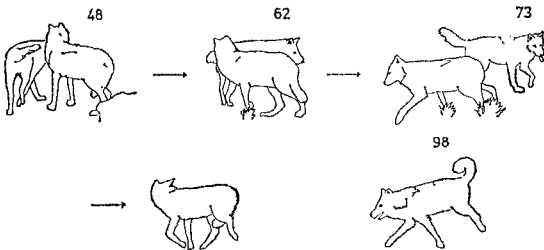
5. Turn-to-Rear/Turn

Relational structure. An example of the Turn-to-Rear/Turn transition is presented in Fig. 13a. As shown in frame 48, the pair begins the transition from a Twist-and-Turn configuration. Frames 62 and 73 represent momentary points in the transition to the Follow configuration in region I (frame 98).

Examples of the Turn-to-Rear/Turn are illustrated graphically in Fig. 14a. In each case initial values of all three variables are in region I. This transition commonly begins from either a Twist-and-Turn or a Stand-Across configuration. The Turn-toRear/Turn initially features an increase in relative distance and orientation and a shift of opposition to the front of D. Relative distance then remains near one wolf-length and the opposition shifts to the extreme rear of D. Both values are characteristic of stable configurations in region II. As indicated by the contrasting examples in Fig. 14a, relative orientation can remain near anti-parallel or change to off-parallel values. The latter orientation indicates that the transition ends in a Follow, the former in a Circle configuration.

It can be seen from the trace in Fig. 11d that the Turn-to-Rear/Turn is distinct from the three preceding transitions because it produces a change from configurations in region II to con-

a. TURN-TO-REAR/TURN



b. WALK-AWAY/WALK

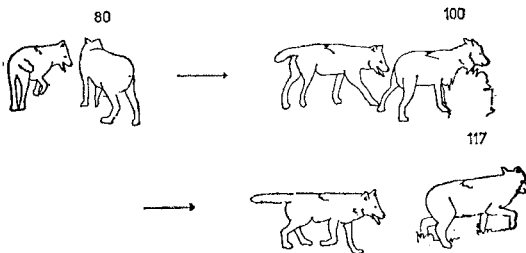


Fig. 13. Artist's illustration of the (a) Turn-to-Rear/Turn, and (b) Walk-Away/Walk transitions. Numerals indicate frame number and fixed reference location.

figurations in region I rather than vice versa. Like the Swivel/Stand-Across, and Lunge/Swivel, however, the Turn-to-Rear/Turn moves through the rear rather than the front of the interaction space.

Individual contributions. The Turn-to-Rear/Turn features greater variability of mechanism than any other transition type. The three movement roles for each interactant that were observed regularly are illustrated in Fig. 15a. The movements diagrammed in Fig. 15a(i) are preceded by a Stand-Across. In this case the Turn-to-Rear/Turn involves: (1) a shift of front by D; (2) a shift of front by S; (3) forward progression by D; and, finally, (4) forward progression by S. The same relational changes (both end points and form) are also achieved by the different combination of individual movements illustrated in Fig. 15a(ii). In this case the transition begins from a Twist-and-Turn configuration rather than a Stand-Across. The transition here involves: (1) the disturbance of the stable configuration by a reversal of direction of shift of front by D; (2) an increase in rate of shift of front by S; (3) the initiation of forward progression by D; and, finally (4) an increase in rate of forward progression by S. The final movement roles that pro-

duce a Turn-to-Rear/Turn are illustrated in Fig. 15a (iii). In this instance the transition begins from a Twist-and-Turn and involves: (1) a disturbance of the stable configuration by a cessation of shift of front and a simultaneous forward progression away from S by D; (2) an increase in rate of shift of front by S as D moves away; and finally, (3) an initiation of forward progression by S. The same pathway in interaction space is accomplished by three regular but distinct combinations of movements by the two

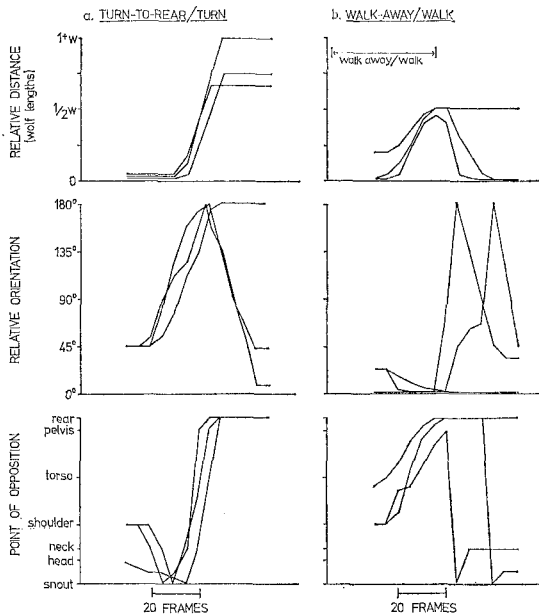
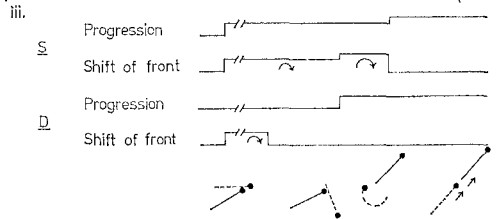
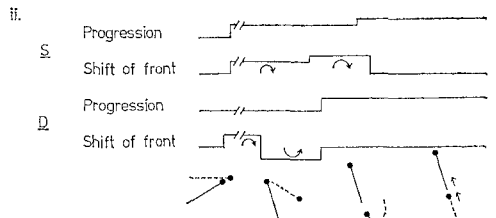
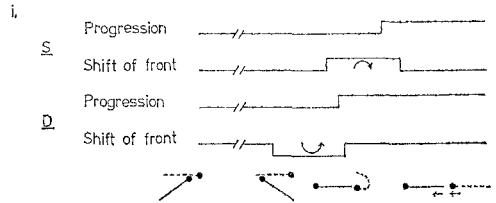


Fig. 14. Changes of the three relational variables during three examples of the (a) Turn-to-Rear/Turn and (b) Walk-Away/Walk transitions.

a. TURN-TO-REAR/TURN



b. WALK-AWAY/WALK

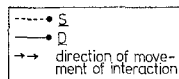
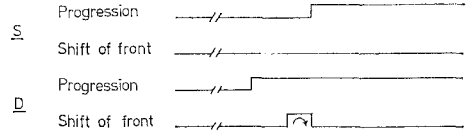


Fig. 15. Movement contributions of each interactant to: (a) Turn-to-Rear/Turn and (b) Walk-Away/Walk. Shifts of front and progressions by each interactant and their temporal relationships are presented for each version of a transition. A schematic illustration of the corresponding relational changes in the interaction produced by these movements by the individuals is presented to assist with the interpretation. (Relative distance not drawn to scale.)

wolves. In each case the transition terminates with a Follow configuration.

6. Walk-Away/Walk

Relational structure. An example of the Walk-Away/Walk transition is presented in Fig. 13b. In frame 80 the pair maintains the Twist-and-Turn configuration in region II. The transition also often begins from the Stand-Across or the Hip-Thrust configurations. In the next frames a transition to relational values in region I and the Follow configuration is achieved via relatively small and direct changes of configuration. The Walk-Away/Walk sometimes flows directly into another transition (Lunge/Swivel) rather than a stable configuration. An example of such an instance is illustrated in the next figure.

Three examples of the Walk-Away/Walk transition are presented in Fig. 14b. Two of the examples follow from the Hip-Thrust and one from the Twist-and-Turn configuration. This difference accounts for the variation in initial values in the graphs. One of the examples leads directly to a Follow configuration and the maintenance of a relatively large distance between the animals, a near parallel orientation, and opposition at the extreme rear of D. In the other two examples, a Lunge/Swivel is initiated immediately after the Walk-Away/Walk and the configuration returns quickly to maintained values in region II. In these latter cases the Follows are represented only as a momentary configuration between the two transitions. In all three cases a characteristic pattern of changes in relational variables is apparent during the Walk-Away/Walk transition itself: an increase in relative distance, the assumption or maintenance of a parallel relative orientation, and a shift of opposition to the rear of D.

The Walk-Away/Walk was the least frequently observed of the transitions. Like the previously described Walk-Up/Stop, this transition leaves a trace in the front portion of the interaction space, and like the Turn-to-Rear/Turn it results in a change from stable configurations in region II to those in region I (see Fig. 11e). This transition to a great extent replicates the Walk-Up/Stop with values changing in the opposite direction (see Fig. 11).

Individual contributions. Figure 15b illustrates the movements of each interactant during the Walk-Away/Walk transition. The disturbances of the Twist-and-Turn, Stand-Across, or Hip-Thrust are the result of movement by D alone. D first walks away from S, progressing slightly

sideways, and makes a shift of front only after the distance between the two interactants has increased. At this point S initiates a forward progression and the Follow configuration begins. The order of these movements and the type of movement shown by each interactant are fixed.

7. Summary of Transitions in Interaction Space

Changes between relatively stable configurations in the two regions of the interaction space (see Fig. 1) were found to be accomplished via a limited number of pathways or types of transitions. That is, the movements of the interactants were coordinated so as to follow specific relational dynamic patterns when changing from one configuration to another. Five transitions were identified: three resulting in changes from configurations in region I to configurations in region II and two producing changes in the opposite direction. The traces of these transitions in the interaction space are presented in Fig. 11. Comparison of these traces reveals that a combination of direction and form of the transition distinguishes clearly between all types.

During extended supplanting interactions, transitions also were observed between stable configurations in the same region. A Follow configuration was changed into a Circle by a simple change in relative orientation; similarly from a Circle to a Follow. An analogous 'simple transition' was observed between the Hip-Thrust and Twist-and-Turn or Stand-Across in region II. Such transitions were described earlier in the examination of the Hip-Thrust.

The overall pattern of individual movement contributions to transitions is analogous to that found for relatively stable configurations. The qualitative aspects of the animal's movement are relatively fixed. Little variation was seen in the type of movement (progression and/or shift of front) made by each interactant or the temporal relations between the movements of the two wolves. The movement role of S in each transition is consistent and specifically quite distinct from that played by D in each transition. Metric features of the same movements, on the other hand, were not constrained to the same extent. Shifts of front occurred in both directions, and the speed of movements by the individuals was variable in all transition types. These aspects of each animal's movements are apparently regulated primarily by the need to conform to the relational patterns outlined above. In contrast to stable configurations, several transitions were found to have a number of equivalent forms in

terms of the movement roles displayed by the interactants (e.g. Turn-to-Rear/Turn). In every type of transition the initial disturbance of the stable configuration results from a movement (or a cessation of movement) by D. In this sense, the transitions are initiated by the displaced animal rather than the supplanter in the extended supplanting interaction.

Once identified and described in detail, all types of stable configurations and transitions were recognized readily in both film records and daily observations. The system of relational movements and individual contributions outlined here was representative of extended supplanting interactions observed during this study (144 filmed sequences; 620 real-time observations). Table I presents the absolute numbers of each relational pattern and of unidentifiable patterns seen during the course of analysis of film records of extended supplantings. It must be remembered that these observations do not reflect a systematic sampling of interactions and should not be seen as a representative distribution of the patterns. Values are affected by variation in the ease with which each type of stable configuration and transition could be photographed. All the same, the table provides a first approximation of the relative frequency of occurrence of the relational patterns.

Discussion

Although ethology was originally conceived as an extension of comparative anatomy (Whitman 1919; Heinroth 1930), morphological studies of behaviour have become less common in recent years, as the focus of interest shifted to the interfaces between behaviour and physiology or behaviour and ecology (see Lorenz 1973). Although of interest in their own right, such studies often divert attention from the organization of behaviour itself. Also, a detailed structural analysis

is often a prerequisite for both functional and causal analysis, in that it specifies the demand on the nervous system and provides the matrix for the analysis of function (Nelson 1973; Fentress 1976a; Golani 1976). The present study describes the morphology of extended supplanting interactions in wolves in a geometric language. The generality of this language makes possible a comparative morphology across a variety of interaction patterns, in ontogeny, and across species. These subjects can all be analysed within one framework.

Although the subject matter of the present study is social behaviour, actual communication between the interactants was not taken for granted at the outset. It emerged, rather, from the description of movement in different frames of reference. Communication is evidenced in this study by a set of spatiotemporal constraints on the behaviour of the individual wolves. Behaviour that initially appeared as a sequence of unintelligible gestures can now be understood in terms of straightforward regularities along several dimensions of movement in real and interaction space. Behaviours that Schenkel (1947) originally described as specialized for communication have been shown, at another level, to involve locomotion by one animal within the complex, ever-changing environment of a moving partner.

At least two characteristics of movement make it a difficult subject for rigorous scientific analysis: its relativistic nature and its dimensional complexity. Movement described relative to a stationary object will be described very differently relative to the simultaneous movements of a social partner. In addition, a single animal has the potential for considerable independent but simultaneous action on a number of movement dimensions (e.g. body parts, turning, progression). The present study acknowledges the

Table I. Number of Occurrences of Relational Patterns of Behaviour in Film Records

Stable configurations		No.	Transitions	
				No
Region I			Region I to II	
Circle		36	Swivel/Stand-Across	11
Follow		85	Lunge/Swivel	14
Region II			Region II to I	
Twist-and-Turn & Stand-Across		101	Walk-Up/Stop	39
Hip-Thrust		18	Turn-to-Rear/Turn	45
			Walk-Away/Walk	16
Total		240		125

Unidentified 11

relativistic nature of movement by describing it simultaneously in relation to the environment and in relation to the moving partner. The dimensional complexity of behaviour is acknowledged by the recording of seven relatively independent variables continuously and simultaneously. Three of these describe behaviour from the point of view of the social partner: the distance, the angle between interactants, and the points of opposition; and the other four describe it in relation to the environment: the progression and shifts of front of each of the interactants. The spatiotemporal relations between these variables form the results of the study. The use of the Eshkol-Wachmann notation system made it possible to handle seven variables at the same time and to extract complex spatiotemporal patterns from them.

Patterning at the Social Level

The analysis of extended supplanting interactions using the three relational variables can be referred to as a 'partnerwise' analysis emphasizing that the description of movement was done relative to a social partner. This partnerwise analysis yielded four relatively stable configurations (see Fig. 8). These configurations involve a strict fixation of opposition, and temporary fixations of values within a specified range of the other two variables. No other configurations are maintained during this type of interaction. Transitions between these configurations are of two types: simple transitions involve a change in only relative orientation (such transitions occur between Follow and Circle, and between Twist-and-Turn and Hip-Thrust) and other transitions between regions that involve a coordinated change along all the three relational variables. Five qualitatively distinct complex transitions were identified (see Fig. 11).

The partnerwise patterns have been treated up to this point as relatively unconnected. The level of analysis employed in the present study is not sufficient for the confident proposal of general rules that might be employed to determine which patterns are employed in any particular situation. It is possible, however, to suggest a principle of transition between relatively stable configurations which may be elaborated in future study. The five transitions outlined in this study abide by the following rules of 'direct' transition: (a) relative distance either increases or decreases with no reversals; (b) opposition shifts along the shortest possible path on D; and (c) relative orientation changes unidirectionally. Simple

transitions between Circle and Follow also follow these rules. The transitions described in this study are consistent outcomes of this single principle of direct transition between the stable configurations. This hypothetical framework reduces five independent patterns of relational movement to a single unifying principle of action requiring 'direct' transitions between stable configurations. (This principle and its relation to the patterns can be visualized best with a pair of pencils acting as 'wolves' on a desk-top.)

Patterning at the Individual Level

If examined separately, progressions and shifts of front of individual interactants yield little obvious regularity. In order to isolate meaningful natural concatenations of movement by the individuals, it was first necessary to partition the flow of the interaction at the social level into relational or partnerwise patterns within which individual contributions could be shown to take place. For example, only after the definition of Twist-and-Turn was it possible to show that it always involves only a unidirectional shift of front by D, and a forward progression combined with a unidirectional shift of front by S. Whereas theoretically each of the partnerwise patterns could involve a variety of individual patterns of progressions and shifts of front, it was found that most of them involve only one such pattern.

The finding, however, that both Walk-Up/Stop and Turn-to-Rear/Turn were associated with more than one, recurrent but different, pattern of individual contribution is of interest in itself. The observation is a clear example in social behaviour of what Lashley (1951) described as motor equivalence. Relations remain constant despite variations in the components. Such a finding suggests, as pointed out by Fentress (1978), that relations among components are often important in understanding behavioural organization and programming, even where these components are in fact different organisms.

The more quantitative characteristics of the movement shown by the wolves in executing the relational patterns were not constrained to the extent of the roles described above. The exact duration, direction, and extent of each individual's movements appear to be regulated primarily by the need to be orchestrated with those of the partner so as to conform to the limits of the relational patterns. This apparent contrast between qualitative and quantitative features suggests that different aspects of a single

movement are simultaneously governed by distinct sets of rules. As such they provide an example of diverse constraints on system components and rules of relations between components, integrating to produce the pattern as a whole (see Fentress 1976b).

In summary, the performance of role-specific individual patterns of S and D is coordinated by the two wolves so as to follow a set of shared rules defining 'permissible' spatio-temporal relationships between their bodies. The interaction is patterned at both the partnerwise and individual levels, and by a coupling between the two. This patterning is empirical evidence of the 'interplay of actions' of the interactants in 'ritualized fighting' first recognized by Schenkel (1947).

It was beyond the scope of the current study to establish the generality of the behavioural organization summarized here. This study provides readily recognizable patterns of movement with which to perform the relevant behavioural comparisons across individuals, pairs, groups of wolves, and time.

The Design of Extended Supplanting Interactions

At present the forces that mould the observed partnerwise and individual patterning are unknown. It is an open question to what extent they are a response to the immediate social environment or represent species-specific internally programmed constraints. We also do not know whether these patterns are resistant to ontogenetic experience or the degree to which they are established by it.

The functional significance of the patterns described here is also unclear, but some possible adaptive features can be pointed out. The most stable coordinates throughout the partnerwise network are the fixated relations of opposition: mouth of S to hindquarters of D during Following and Circling, and flank of S to front of D during Twist-and-Turn and Hip-Thrust. During the first two fixations relative distance is never smaller than half a wolf length; and during the second two, distance is maintained at contact or near-contact. During Following and Circling, the mouth and teleceptors of S are maintained at a darting-distance-for-bite at D's (potentially harmless) hindquarters. Indeed, the only frequent wounds observed during the study period were to the extreme hindquarters of D. The distance of half a wolf-length is also just appropriate for the performance of what could be interpreted as a 'blocking technique' from S's potential bite:

both Lunge/Swivel from Following and Swivel/Stand-Across from Circling involve a rapid shift of S's mouth from D's hindquarters to the front of D's mouth. During Twist-and-Turn, S and D are maintained at the appropriate distance for Hip-Thrusts. When these are applied vigorously by S, they may result in D's loss of balance and S's subsequent biting at D's hindquarters. Since, during Hip-Thrusts, D squats on the hindquarters, S's potentially harmful thrusts lose most of their impact. Also, at such times D's mouth opposes at near-contact or contact the flank of S's head or mouth, perhaps providing defensive potential. Walk-Away/Walk and Turn-to-Rear/Turn involve either a termination of the interaction by increase in inter-animal distance or opposition and 'release' of the relationship of opposition, or re-establishment of the inter-animal distance appropriate both for a darting-to-bite by S and a 'blocking exercise' by D. This distance can also be reduced relatively slowly by a Walk-Up/Stop.

One relational configuration that is only rarely observed during extended supplanting interactions is a face-to-face, anti-parallel, at near-contact or contact configuration. When this rare configuration is observed, the two wolves often rear up on their hindquarters, pushing forward with all their weight, leaning on the partner's shoulders with forequarters, and biting extensively. S eventually pushes over D, who loses balance and falls on her back or side, as S commences to bite. This class of relational configurations, regularly described by ethologists as a 'fight', is beyond the scope of the present paper. However, extended supplanting interactions appear to be structured so as to both avoid and furnish the opportunity for the performance of this class of relational configurations. Possibly, for both S and D, extended supplanting furnishes the opportunity to both avoid actual fighting and/or attain a configuration that leads into it. Such fights may ensue in the re-establishment or long-term reversal of the respective social roles.

Acknowledgments

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