

- Lorenz, K. 1952 Balz und Paarbildung bei der Stockente C 626(16 mm Film). Göttingen: IWF
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INSTITUT FÜR DEN WISSENSCHAFTLICHEN FILM
HOCHSCHULFILM C 626/1952

Courtship and Pair Formation in the Mallard
(*Anas platyrhynchos* L.)

By
Prof. Dr. K. LORENZ
(with 13 figures)

Göttingen 1982

Comments on IWF University Series Film C 626/1952
Courtship and Pair Formation in the Mallard (*Anas platyrhynchos* L.)

By

Prof. Dr. K. Lorenz (translated from the German by W. M. Schleidt¹⁾)

The film starts with scenes from the social courtship of the drakes. With increasing intensity of the social interactions, pair formation occurs, followed later in the season by copulation with foreplay and afterdisplay. These scenes are followed by scenes of fighting drakes, and the film closes with the attempted rape by a drake of a female who is mated to another drake.

This film is intended for use in university teaching. This 16mm version runs for 9 minutes at 20 frames per second and comprises 81 m.

I. General Introductory Remarks

The fixed action patterns (FAPs) of ducks were one of the first subjects of ethology. From these behaviour patterns Oskar Heinroth was the first to discover that FAPs can be treated like morphological features, and that the concept of homology is therefore applicable. The innate behaviour patterns of courtship and pair formation were especially used by this investigator in his phylogenetic comparisons. The surface feeding ducks - Anatinae - are the best known group of ducks, and within this group most research has been done on the mallard.

As in the black grouse, the ruff, and other birds, we find in the mallard a social courtship of the males. The females choose their mates among the socially displaying drakes by performing a specific ceremony and duce them, by specific behaviour patterns, to enter into a pair bond. This is only indirectly related to the actual copulation which occurs much later in the season.²⁾ Although the pair bond is

¹⁾ Dr. Frank McKinney and Dr. Uli Weidmann, both experts on mallard behaviour, kindly checked this translation, and provided additional comments, and references; their additions are marked with their initials. The list of sequences, scenes and behaviour patterns was prepared by Ms. Donna Ireton, Mrs. Jo Ann Finley and Ms. Terry Thompson.

²⁾ Note that in the northern hemisphere pairing and copulation occur from September onward. What is meant is that copulations that lead to the fertilization of eggs do not occur until spring (F.M.).

maintained for life,³⁾ mated drakes continue to participate in the social courtship. This film presents a nearly complete inventory of the FAPs of social courtship and pair formation in both sexes, as well as the FAPs of fighting in the drakes, and the strange attempts of mated drakes to rape females other than their mate.

II. Specific Comments on the Film

Lockruf⁴⁾

Attraction Call

Versammlung der Erpel

Assembly of the Drakes

Einleitendes Schütteln und Grunz- pfiff

Introductory Shake and Gruntwhistle

The characteristic courtship assemblies start immediately after both sexes have finished their summer molt, and the drakes show their nuptial plumage. The drakes assemble in remarkable numbers at certain preferred bodies of water. By giving the extended attraction call, which is emitted with the neck held straight up, the drakes attract other drakes as well as the females.

The body stance of the drakes reveals the onset of higher levels of courtship motivation. The plumage on the head is ruffled, the head is drawn back between the shoulders and, because of the general ruffled state of the body plumage, the drakes float high on the water surface (Fig. 1). In this introductory phase of the social courtship



Fig. 1. Initial stance of a drake participating in social courtship.

one can often see a concentration of drakes in the center of the assembly, while the females form a ring of attentive spectators.

3) According to F.M. and U.W., the pairbond is not maintained for life, though sometimes the mates of one season re-pair in the next one (see Dwyer et al. 1973). As a rule the pair breaks up soon after the female starts to incubate.

4) German headings of the film.

Then the actual courtship starts. The first of its movements is the lateral billshake (Fig. 2) which certainly has its origin in a displacement activity (Tinbergen). The higher the action-specific excitation rises, the higher this introductory bill movement virtually pulls the drake from the water's surface.

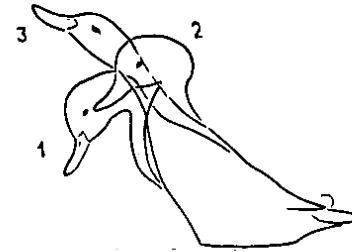


Fig. 2. Schematic representation of the introductory shake movement.⁵⁾

As a certain threshold is reached, the first actual courtship movement appears, the so-called gruntwhistle. Evolutionarily speaking, this movement is derived, without a doubt, from the introductory shake, as can be proven by the comparative study of certain related species. The gruntwhistle starts as a shake. The drake bends over so that his bill touches the water and at that moment gives a lateral jerk of the bill which ejects a series of water droplets.⁶⁾ The next moment the drake raises his breast sharply from the water, at first without bringing up his head, which results in a strange stance with the neck curved forward-down and the head held low (Fig. 3). This arched position apparently puts tension on the trachea as well as on the bony resonator at the syrinx of the drake, since the piercing whistle is emitted exactly at the climax of this arched position. Subsequently, the head is brought up and the body falls down in the normal horizontal position, just as a low pitch grunt becomes audible (thus the name of this movement).⁷⁾

5) More precisely the introductory shake involves two distinct FAPs: one upward shake (Fig. 2) is followed by 1 to 3 head-flicks - in which the body is not lifted out of the water. For more details see McKinney, 1965, and Simmons & Weidmann, 1973.

6) The directional bias of the jerk causes the droplets to be flung toward the addressed female (von de Wall, 1963, Simmons & Weidmann, 1973).

7) U.W. suggests the use of water-flick as a label for the movement to distinguish it from the associated sound, which actually is a whistle-grunt (see Cramp & Simmons, 1977).

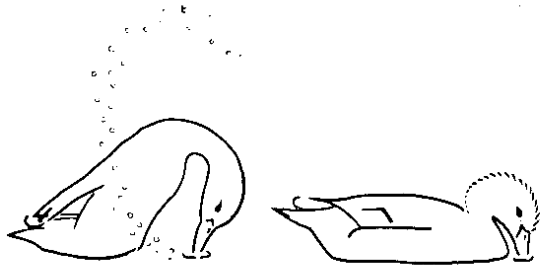


Fig. 3. Two phases of the gruntwhistle movement. Note the curved array of water droplets.

It can be shown that the gruntwhistle has a lower threshold than the two courtship patterns discussed later.⁸⁾ At a higher level of excitation, several of the assembled drakes perform this courtship pattern, always in synchrony.⁹⁾ At lower levels only one drake performs at a time, and in this case the gruntwhistle occurs several times more often than the other courtship movements.

Ab-Auf-Bewegung
Rüb-Rüb-Palaver

Down-Up Movement
Rab-Rab Palaver

At higher levels of the action specific excitation⁸⁾ we observe either the down-up or head-up-tail-up. Which one of these two is executed depends to a large extent on the presence of aggressive motivation, in addition to courtship excitation, although other factors which are not well understood so far may play a role. In the presence of an aggressive undertone a strange, brief movement occurs, in which the body is tilted forward and in a flash the bill is dipped into the water and brought up again, pulling up a little column of water (Fig. 4). This, as well as a brief flash of the white of the neck ring which broadens conspicuously when the bill is pulled upward, may provide an optical cue for the females.

8) This refers to Weidmann 1956, who made these observations while working under Lorenz at Buldern in 1951/52.

9) This statement is erroneous, apparently due to a misunderstanding, and could well refer to synchrony in the head-up-tail-up or in the down-up (see Weidmann, 1956, Johnsgard, 1960, Weidmann & Darley, 1971b).



Fig. 4. The "down-up" of the drake. Note the column of water drawn from the surface.

Subsequent to this movement, sometimes also before its execution, the drakes float with the heads raised horizontally and emit quickly and intensively their bisyllabic contact call "rab-rab, rab-rab". This expression movement infallibly indicates a rising level of aggression. It is especially visible whenever two drakes threaten each other. It is not uncommon that the down-up and rab-rab are suddenly followed by a physical attack.

Kurzhoch-Werden

Head-Up-Tail-Up

The third and least common courtship movement of the drake consists of a simultaneous raising of head and tail, so that the drake arches like a U, and becomes so short that the wings have to be raised at the shoulder joint in order to allow sufficient leeway for the movement of the vertebral column (Fig. 5). This raising of the elbows displays the colors of the speculum and reveals the otherwise partially occluded circular tail-covers.



Fig. 5. The "head-up-tail-up" of the drake. The same climactic phase is shown from different angles.

Furthermore, the extreme uptilt of the tail exposes a striking white area on the rear of the rump, and the brown chest and the white neck ring also become especially conspicuous so that the drake presents a most spectacular sight.

This courtship movement relates - more than the others - to the presence of a particular female. Immediately after a head-up-tail-up the drake, in a sudden movement, turns his head toward one particular female (Fig. 6). Then, starting with a strange, exaggerated initial movement of bridling, a rearing with the head pulled back,¹⁰⁾ he

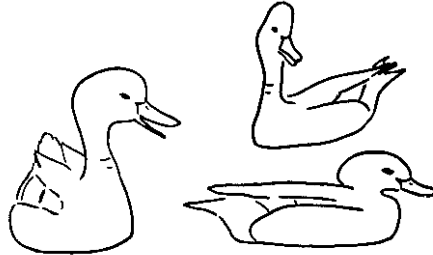


Fig. 6. The "turn-head-to-female", immediately after the head-up-tail-up.

propels his head and neck forward and swims in a circle around this female in a movement called nod-swimming (Fig. 7). It terminates with a raising of the head and turning the back of head toward the female (Fig. 8), while the feathers on the sides of the head are sleek and those on the back of his head and nape are ruffled so that in this area a velvety black area, surrounded by iridescent green, becomes visible.



Fig. 7. The "nod-swimming" of the drake, linked to head-up-tail-up and "turn-back-of-head" toward the female.

¹⁰⁾ U.W. agrees with Johnsgard (1960a) that bridling is extremely rare during the 'head-up-tail-up complex' (the sequence head-up-tail-up, turn-head-to-female, nod-swimming, turn-back-of-head).

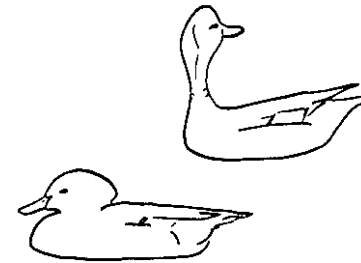


Fig. 8. The "turn-back-of-head" to female of the drake without "head-high", in this form commonly coupled to nod-swimming.

Since the two last components of this behaviour, namely bridling and turn-back-of-head toward female, are also used in the display after copulation, it is tempting to assume that these movements are more directly related to copulation.

Scheinputzen und Hetzen

Mock-Preening and Inciting

When the social courtship has been performed for several weeks, the females which are still unmated begin to choose a mate among the displaying drakes. Instead of arousing the males by nod-swimming to continued courtship (Fig. 9), the female swims toward one particular male and performs the FAP called "inciting". This is a highly exaggerated and ritualized turning of head and bill backward over her shoulder.

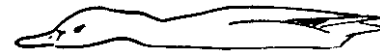


Fig. 9. The "nod-swimming" of the female.

der, even when there is no one in this direction who could be considered as an enemy (Fig. 10). When the drake is inclined to accept the female as his mate, he replies to the inciting by performing head-high or rab-rab-palaver or - at highest state of arousal - by ritualized displacement-preening, the so-called "mock-preening" (Heinroth). The bill is pushed under the wing and drawn across the

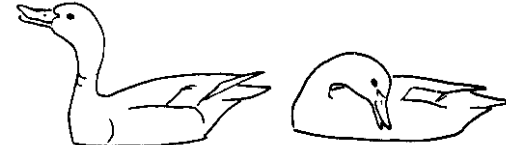


Fig. 10. "Inciting" of the female and "head-high" of the male.

shafts of the secondaries so that the feathers are moving and, through their colorful vanes, emit a strong visual stimulus (Fig. 11). If the drake does not respond to the inciting of the female, it is not uncommon that she swims toward another drake and tries to incite him

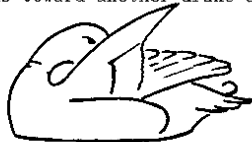


Fig. 11. The "mock-preening" of the drake. An audible noise is produced when the bill is drawn across the shafts of the secondaries.

into an attack on the one who has rejected her just before.¹¹⁾

Paarung mit Einleitung und Nachspiel

Copulation with Foreplay and Afterdisplay

Copulation is usually initiated by the female because her sexual motivation is generally higher than that of the drake.¹²⁾ The movement which provides for social facilitation consists of a vertical up and down movement of the head, bill held horizontally, in which the downward phase is considerably faster than the upward phase (Fig. 12). In ethology this FAP is generally called pumping. It has been observed in literally all Anatinae as foreplay and can most likely be derived evolutionarily from an intention movement for the prone posture, as it is commonly found in the act of copulation. The function of this movement is without doubt the mutual stimulation of the

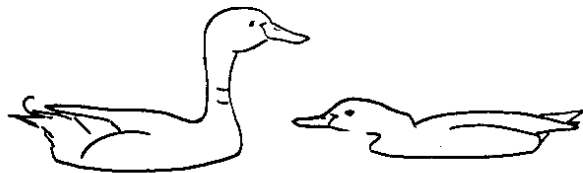


Fig. 12. "Pumping" as foreplay to copulation.

¹¹⁾ F. M. points out that so far there is no quantitative support for this view.

¹²⁾ F. M. and U. W. have reservations about this statement, and point out that either sex may start pumping, but pair copulation follows only when female joins in and then adopts the prone posture.

mates and the synchronization of their reactions. One can see clearly that the more intensely "pumping" mates stimulates his partner, while the less active one seems to slow down the first so that the subsequent FAPs of copulation take place in perfect synchrony.

After the actual copulation, which is not markedly different from that in other birds, the pair hangs together for a moment.¹³⁾ Then the drake performs a rather complicated afterdisplay. It starts with a very pronounced "bridling", in which the female is sometimes passively involved, since the drake continues to hold on to the female's nape (Fig. 13). Immediately afterwards he rushes away "nod-swimming"

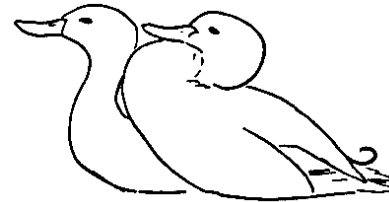


Fig. 13. The "bridling" of the drake after copulation.

in a circle around the female. It ends with the "turn-back-of-head" in which a velvety black area, surrounded by green, is turned toward the female.

These later parts of the afterdisplay are identical to those movements which follow the head-up-tail-up.

Kampf der Erpel

Fighting of the Drakes

Serious fighting among drakes is observed only late in the season in spring,¹⁴⁾ when the social courtship is fading out,¹⁵⁾ most pairs are mated, and remaining bachelors court mated females. The drakes start out by grabbing each other's breast feathers, and probe each other like wrestlers before grappling starts. This is followed by a

¹³⁾ The Anatidae are, as is generally known, among those few bird groups in which the male has a penis.

¹⁴⁾ U. W. remarks that prolonged fights (including "chest-fights") are occasionally occurring in autumn.

¹⁵⁾ U. W. has observed most spring fights at the height of the period of social courtship in February and March.

duel of blows with one wing, while the other wing is raised over the back for balance. When one drake finally gives up and tries to leave, the victor not uncommonly holds on to his feathers and is dragged along.

Vergewaltigungsversuch

Rape Attempt

As the females get close to laying their eggs, a new behaviour appears in the drakes. Strangely enough, only the drakes who are solidly engaged in a pair bond,¹⁶⁾ and owners of a breeding territory, respond to the appearance of any strange female by attempting to rape her. This is rarely successful¹⁷⁾ since the female attempts to escape at all cost, and her mate defends her well. Geyr von Schweppenburg (1924) hypothesizes that the adaptive significance of these rape attempts, which lead sometimes to grotesque scenes, lies in the dispersal of mallard pairs over a larger area, in order to avoid high densities of breeding pairs.

(Submitted 13 March 1952)

The film was produced 1951/52. Edited for use in university teaching and published by
Institut für Film und Bild in Wissenschaft und Unterricht, Division for University and Research, Göttingen (Director: Dr. Ing. G. Wolf)
Assistant Producer: G. Bekow

16) U. W. points out that only paired males engage in rape.

17) F. M. holds that successful forced copulation is a regular thing and, in captives, has been shown to result in fertilization of eggs.

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List of Sequences, Scenes, and Behaviour Patterns

Code:

M - male R - right LO - lower C - center
 F - female L - left UP - upper (act not completed)
 H - horizontal V - vertical

<u>Scene</u>	<u>Frames</u>	<u>Animal</u>	<u>Description</u>
			Lockruf Versammlung der Erpel Einleitendes Schütteln Grunzpfiff
			Attraction call Assembly of the drakes Introductory Shaking (head shake, head flick) Grunt whistle
1	1-38 1-51 52-88	F, M F	Flight to pond Landing
2	89-291	M	Swimming, Rab, entrance of several other ducks into scene
3	292-428	4F, 3M	Swimming
4	429-605 429-550 551-605	6M UP L M	Swimming Preen
5	606-803 612-622 615-626 629-676 681-695 715-734 621-721 734-741	5M, F UP L M R M L M UP R UP R LO L M UP R	(Tail-shake), head shake-V Head-shake-V Tail-shake Bill-dip Bill-dip and head-shake-H Swim Head-shake-H
6	804-1156 804-860 824-834 834-865 865-895 942-957 804-860 806-825 830-865	C M#1 UP M#2 LO R M#3	(Tail-shake) Head-shake-V Grunt-whistle Tail-shake Head-shake-V (Tail-shake) Bill-dip Grunt-whistle Tail-shake Head-shake-H Head-shake-H Head-shake-H
7	959-970 1081-1097 1036-1046 1157-1258 1157-1206	M#4 UP M	Head-shake-H Head-shake-H Head-shake-H (Head-flick) (tail-shake)

Scene	Frames	Animal	Description
8	1259-1459		
	1259-1333	R M#1	(Tail-shake)
	1291-1313		Head-flick
	1325-1337		Head-shake-V
	1349-1359	LO L M#2	Head-shake-V
	1372-1448		Tail-shake
	1450-1460		Head-shake-H
	1425-1440	F#3	Head-shake-H
9	1460-2000		
	1460-1493	Front M#1	Head-flick with (tail-shake)
	to 1509		
	1509-1520		Bill-dip
	1528-1566	Rear M#2	Tail-shake
	1636-1757		Tail-shake
	1673-1675		Wing-flick-L
	1681-1683		Wing-flick-R
	1777-1779		Wing-up
	1794-1858		Tail-shake
	1828-1850		Head-shake-V
	1906-1955		Tail-shake
	1944-1984		Head-flick
1959-1981	M#3	Bill-dip	
1981-2000		(Tail-shake)	
10	2001-2188		
	2015-2054	M	Head-flick
	2029-2091		Tail-shake
	2126-2131		Wing-flick-R
11	2189-2356		
	2189-2282	M	(Tail-shake)
	2226-2259		Head-flick
12	2357-2493		
	2357-2376	LO M#1	Head-shake-V with (tail-shake)
	2440-2470		Head-flick
	2357-2438	Rear M#2	Tail-shake
	2379-2415		Head-flick
13	2494-2600		
	2494-2536	M#1	(Tail-shake)
	2497-2526		Head-flick
	2531-2570	Rear M#2	Grunt-whistle
	2536-2577		(Tail-shake)
	2597-2600		(Head-shake-V)
14	2601-2705		
	2627-2662	M	Grunt-whistle
	2654-2696		(Tail-shake)
15	2706-3025		
	2706-2809	UP M	(Tail-shake)
	2759-2797		Head-flick
	2805-2821		Head-shake-V
	2868-2885		Head-shake-H
	2937-2952		Head-shake-V
	2952-2985		Grunt-whistle
	2966-2999		Tail-shake
	3010-3025		Rab

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Scene	Frames	Animal	Description
16	3026-3161		
	3067-3085	UP R M#1	Head-shake-V
	3079-3088		Tail-shake
	3095-3123		Grunt-whistle
	3112-3135	LO R M#2	Tail-shake
	3113-3115		Rab
17	3162-3267		
	3162-3195	UP C M	Grunt-whistle
	3173-3222		Tail-shake
	3244-3255		Head-shake-H
	Ab-Auf-Bewegung		Down-up
	Räb-Räb-Palaver		Rab-Rab-Palaver
18	3361-4073		
	3361-3419		General swim and Rab
	3420-3449	UP M#1	Bill-dip
	3474-3494	C M#2	Bill-dip
	3500-3520	L M#3	Chase and shove
	3591-3604	C M#4	Head-shake-V
	3723-3761		Down-up with Rab
	3608-3628	C L M#5	Bill-dip
	3634-3666	UP R F#7	(Bill-dip)
	3651-3678	UP C #8	Bill-dip
	3707-3761		Down-up
	3817-3838	Rear M#9	Bill-dip
	3864-3886		Bill-dip
	3891-3904		Head-shake-H
	3923		Rab
	3992-4011		Bill-dip
3817-3882	L F#10	Inciting	
3925-3960	R F#11	Inciting	
4000-4040		Inciting	
3925-3938	Front M#12	Head-shake-V	
3940-3997		Down-up with Rab	
4069-4073		(Tail-shake)	
3978-4000	L F#13	Bill-dip	
19	4074-4356		
	4074-4307	M#1, M#2	Fighting
	4227-4245	Front M#3	Head-shake-V
	4293-4340		Down-up
	4323		Rab
	4307	M#4	Enters fight
20	4357-4599		
	4357-4368	M#1, M#2	(Down-up) with Rab
	4429-4475	F	Inciting
	4458-4485	M#3	Bill-dip
	4564-4580	M#1	Bill-dip

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Scene	Frames	Animal	Description	
21	4600-4829	M#1	Head-shake-V	
	4617-4626		Grunt-whistle	
	4642-4675		Tail-shake	
	4665-4689	F Rear C M#2	Down-up with Rab	
	4725-4766		Head-shake-V	
	4641-4654		Head-shake-H	
	4668-4683		Tail-shake	
	4682-4729		Head-shake-V	
	4713-4729		Down-up	
	4729-4769		Rab	
	4747-4776		Bill-dip	
	4791-4816		(Head-shake-H)	
	4826-4829		Head-shake-H	
	4670-4679	(Tail-shake)		
	4680-4717	M#3	Down-up with Rab	
	4732-4771		Down-up with Rab	
	4731-4771	M#4	Chases M#3	
4771-4819				
22	4830-5069	M#1, M#2 M#3	Simultaneous Down-up with Rab	
	4971-5018		(Grunt whistle) with (tail-shake)	
	4984-5018			
Kurzhoch-Werden		Head-up-Tail-up		
23	5143-5206	M	Head-shake-V	
	5144-5156		Head-up-Tail-up	
	5165-5185		Rab	
	5174-5175		Turn head to female	
	5174-5194	F	Inciting	
	5171-5201		(Nod-swim with Rab)	
	5194-5206			
24	5207-5351	M	Nod-swim	
Scheinputzen und Hetzen		Ritualized Preening and Inciting		
25	5445-5825	M	Bill-dip	
	5456-5477		Head-shake-H	
	5477-5483		Preen	
	5483-5509		Tail-shake	
	5500-5514		Bill-dip	
	5514-5529		Bill-dip	
	5552-5571		Head-shake-H	
	5570-5577		Preen	
	5577-5602		Tail-shake	
	5593-5602		Bill-dip	
	5605-5641		Head-shake-H	
	5641-5646		Head-shake-H	
	5646-5676		Preen with tail-shake	
	5676-5699		Bill-dip	
	5453-5804		R F#1	Inciting
	5519			reck F
	5526-5575		LO F#2	Inciting

Scene	Frames	Animal	Description	
Paarung mit Einleitung und Nachspiel		Mating with Introduction and After-Display		
26	5922-6308	M	Mount	
	5953		Grasp F neck	
	6014		Tail-shake	
	6014-		Dismount	
	6098-6119		Grasp F neck	
	6125		Bridle	
	6126-6139		Nod-swim	
	6139-6233		(Tail-shake)	
	6268-6281		(Dunk-"bathing")	
	6141-6281		R M	(Wing flicks and tail shake)
	6008-6137			
27	6309-6985	R M#1	Pumping 18 times	
	6309-6613		Mount	
	6614		Grasp F neck 2 times	
	6638-6761		Bridle	
	6761-6777		Nod-swim	
	6777-6850		Bathe	
	6943-6985		Inciting	
	6309-6428		F	Pump, incite
	6428-6470			Incite, pump
	6470-6560			Stretch neck
	6604-6761		Background M,F	Bathe
	6804-6985			Bill-dip
	6609-6623			Rab
	6623			Bathing
6309-6497	Background F	Preening		
6803-6985		Wing flap		
6497-6556				
Kampf der Erpel		Fighting of Drakes		
28	7073-7355	M#1, M#2	Bill jousting	
	7074-7355			
29	7356-9918	L M	Fight on bank with wing flaps, grasping necks	
	9903-9917		(Tail-shake) while walking	
30	9919-10150	M#1, M#2	Landing in water, M#1 chases M=2	
	9991-10040		Wing-flap and tail-shake	
	10040-10060	Front M	Head-shake-V	
	9995-10065		Wing-flap	
	10097-10114		Head-shake-V	
Vergewaltigungs-Versuch		Rape Attempt		
31	10242-10346	2M, 1F	Both males chase female	
32	10347-10722	2M, 1F	Both males attempt to mount female, another male enters scene	
	10347-10562			
	10575-10721		Female flies away, pursued by one male, other two males fight	